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REVIEW OF THE SUBGENUS *CATONOTUS* (PERCIDAE)
WITH DESCRIPTIONS OF TWO NEW DARTERS OF
THE *ETHEOSTOMA SQUAMICEPS* SPECIES GROUP

By

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INTRODUCTION

The Cumberland and Tennessee drainages together with tributaries of the lower Ohio River possess one of the most diverse fish faunas in North America. Many species native to these drainages are endemic. The subgenus *Catonotus* is no exception to the pattern of diversity in this region. With the exception of *Etheostoma flabellare* all of its members are restricted to the Cumberland, Tennessee, and lower Ohio river drainages.

Prior to 1978, accounts of the spottail darter, *Etheostoma squamiceps*, considered it to be a single variable species. Howell and Dingerkus (1978) recognized the diversity in *E. squamiceps* when they described a highly distinctive species, *E. neopteron*. Although their study was not inclusive of the total range of *E. squamiceps*, they considered the possibility of additional undescribed forms masquerading under the now more restrictive taxon, *E. squamiceps*. Braasch and Page (1979) additionally recognized diversity in the spottail darter and described *E. olivaceum*, a distinctive species known from the Caney Fork system since the 1960's. Further, these authors had independently reached the same conclusion as Howell and Dingerkus (1978), that the spottail darter represents a polytypic taxon.

It is the purpose of this paper to examine morphological variation of *E. squamiceps* and its relatives. Two new species of this group are described herein. A brief review of other *Catonotus* is presented as well as hypotheses of phylogenetic relationships and biogeography.

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METHODS

Methods of data collection employed in this study follow Braasch and Page (1979). Complete locality data of materials examined are available from the authors. Museum acronyms are identified in acknowledgments, except for the following: AMNH = American Museum of Natural History, BMNH = British Museum of Natural History, MCZ = Museum of Comparative Zoology, and SU = Stanford University. The abbreviation MEB refers to Marvin E. Braasch collections. The following abbreviations are used throughout the text: SL = standard length, HL = head length, BD = body depth, CPD = caudal peduncle depth, PreOL = preorbital length, HL = head length, EW = eye diameter, DFB = spinous dorsal base length, DFH = spinous dorsal height, P₁L = pectoral fin length, P₂L = pelvic fin length. Analyses of phylogenetic relationships involved methods of outgroup comparison and parsimony. Our use of this method was aided through the computer program PAUP, Phylogenetic Analysis Using Parsimony, provided by David Swofford of the Illinois Natural History Survey, Champaign. Since the subgenus *Catonotus* has been considered phylogenetically close to the subgenus *Oligocephalus* this group was used as the primary outgroup. However, since *Oligocephalus* has recently been split up taxonomically, we also made comparisons with other species of *Etheostoma*, as well as *Percina* and *Ammocrypta*.

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SUBGENERIC SYNOPSIS

Catonotus Agassiz, 1854, Amer. Journ. Sci. and Arts 17:305

Type-species *Catonotus lineolatus* Agassiz, 1854 by monotypy

Richia Coker, 1926, Bull. Bur. Fish. 42:106

Type-species *Richia brevispina* Coker, 1926

Invalid name—preoccupied by *Richia* Grote, 1887 (Lepidoptera)

Richiella Coker, 1927, Copeia 102:18

Type-species *Richia brevispina* Coker

Replacement for *Richia* Coker

TAXONOMIC HISTORY OF THE SUBGENUS

Rafinesque, in 1819, described *Etheostoma flabellaris*, the first species of the group now known as *Catonotus*, and placed it along with *blennioides* and *Sciaena caprodes* in the new genus *Etheostoma*. Rafinesque did not designate types for either the new genus or species (Collette and Knappe, 1966). The genus *Catonotus* was erected by Agassiz in 1854, when he described *C. lineolatus* and designated *E. blennioides* as type-species for Rafinesque's *Etheostoma*. Putnam (1863) then added *C. kennicotti* from southern Illinois to the genus. Jordan (1875) placed *flabellare* in *Catonotus* and merged the genus *Nothonotus* Agassiz with it. Jordan (1877a) then described *E. squamiceps*, placed it in this group, and subtracted *Nothonotus* from *Catonotus*. Ignoring Agassiz's work, as well as Jordan's earlier papers, Cope and Jordan (in Jordan, 1877b, p. 51) designated *flabellare* as the type-species for *Etheostoma*, thus replacing *Catonotus* with *Etheostoma* for the subgenus. Jordan and Evermann (1896) merged many existing darter genera into the single genus *Etheostoma* Rafinesque, retaining the former genera as subgenera. The name *Catonotus* was restored by Opinion 14, International Comm. Zool. Nomen. 1910 (see Hemming, 1947 for discussion of Opinion 14) and has been used as a subgenus by Bailey and Gosline (1955) and Page (1975a, 1981) in their systematic work on darters.

Relationships of the barcheek darters, *E. virgatum* Jordan and *E. obeyense* Kirsch, to *Catonotus* were not early recognized. They were placed in various subgenera (or genera) and were not formally listed as *Catonotus* until Bailey and Gosline's (1955) review of the darter subgenera.

Collette (1965) divided *Catonotus* into two species groups—the *E. flabellare* group (*flabellare*, *kennicotti*, and *squamiceps*) and the *E. virgatum* group (*virgatum* and *obeyense*). Kuehne and Small (1971) added *E. barbouri* as a third member of the *virgatum* group and presented a

detailed diagnosis for the subgenus. Page (1975a) further subdivided the subgenus into three species groups—the *flabellare* group (*flabellare* and *kennicotti*), the *squamiceps* group (*squamiceps*), and the *virgatum* group (*virgatum*, *obeyense*, and *barbouri*) based on secondary sexual characteristics and breeding behaviors.

Since 1976, four additional *Catonotus* have been described; *smithi* Page and Braasch, 1976 and *striatulum* Page and Braasch, 1977 of the *virgatum* group; and *neopterum* Howell and Dingerkus, 1978 and *olivaceum* Braasch and Page, 1979 of the *squamiceps* group. The two additional species of the *squamiceps* group described herein and an undescribed species of the *flabellare* group (being studied by Dr. Robert Jenkins) brings the total number of *Catonotus* species to twelve.

THE SUBGENUS *Catonotus* AGASSIZ

Diagnosis—The following diagnosis is modified from Kuehne and Small (1971) and Braasch and Page (1979): lateral line incomplete and straight; preoperculomandibular canal pores 8-11; branchiostegal rays usually 6; body fairly elongate; snout pointed; premaxillary frenum present; vertebrae 32-37; first dorsal fin low; dorsal spines 7-11 and with fleshy tips in breeding males; anal spines 2, the first thicker than the second and more than half the length of the first ray; breeding tubercles absent; anus not encircled by fleshy villi; genital papilla of females flat and not bifurcated.

KEY TO SPECIES GROUPS

1. Nape and/or breast scaled, base of caudal fin with vertical row of 3 dark spots *E. squamiceps* group
Nape and breast naked, base of caudal fin without spots 2
2. Body and fins with red and blue coloration; cheeks with red and white iridescent diagonal bar; fleshy knobs on dorsal fins small and opaque; infraorbital canal pores 6 or fewer *E. virgatum* group
Body lacking red or blue colors; no brightly colored bar on cheeks; large round fleshy golden knobs present on tips of dorsal spines of males; infraorbital pores 7 or more *E. flabellare* group

ETHEOSTOMA *SQUAMICEPS* SPECIES GROUP

The *E. squamiceps* species group is a group of five closely related usually allopatric species in the lower Ohio, Cumberland, and Tennessee river drainages from southern Illinois and Indiana south to northern Mississippi and Alabama. Species are moderately large to large *Catonotus* (maximum body size = 85 mm SL) characterized by having three dark spots at base of caudal fin, scales on nape, prepectoral, and breast (and usually on cheeks and opercles), body and fin coloration not chromatic, infraorbital canal complete or incomplete with 7 to 8 pores, and dorsal fin spines with fleshy knobs in both males and females. The most important

characters distinguishing members of this group are coloration and shape of dorsal fins of nuptial males. Since all species lack bright colors, apparently fin coloration and shape are used for species recognition. These characters are of taxonomic use only during the height of the breeding season.

Etheostoma squamiceps JORDAN

Spottail Darter

Figs. 1, 2, 3.

Etheostoma squamiceps. Jordan, 1877:11-12 (original description, Russellville, KY)

Claricola squamiceps. Jordan, Evermann and Clark, 1930:292 (check-list of fishes)

Catonotus squamiceps. Gerking, 1945:94 (status in Indiana)

Poecilichthys squamiceps. Moore and Cross, 1950:145-146 (separation of *E. squamiceps* and *E. parvipinne*)

Types—*Etheostoma squamiceps* was described from two specimens from Russellville, Logan Co., Kentucky. The exact locality is unknown. It could have been from either the Green River system of the Ohio drainage or the Red River system (Cumberland drainage). Since the form *E. squamiceps* (as used herein) is the only species of the *E. squamiceps* group found in the Green or Red rivers, we restrict the types of Jordan to this form. Lectotype designated by Collette and Knapp (1966): 59 mm SL male

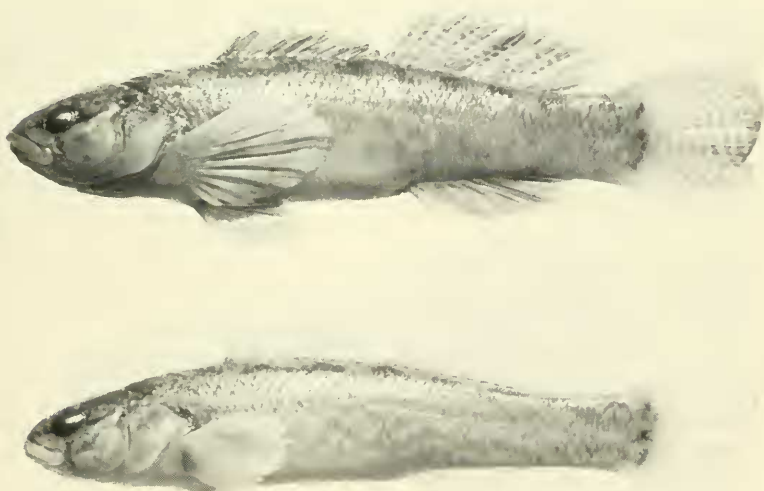


FIGURE 1. *Etheostoma squamiceps*. Top, male 61.6 mm SL; Bottom, female 55.9 mm SL (INHS 75747, Wabash R. System, Posey Co., Indiana).

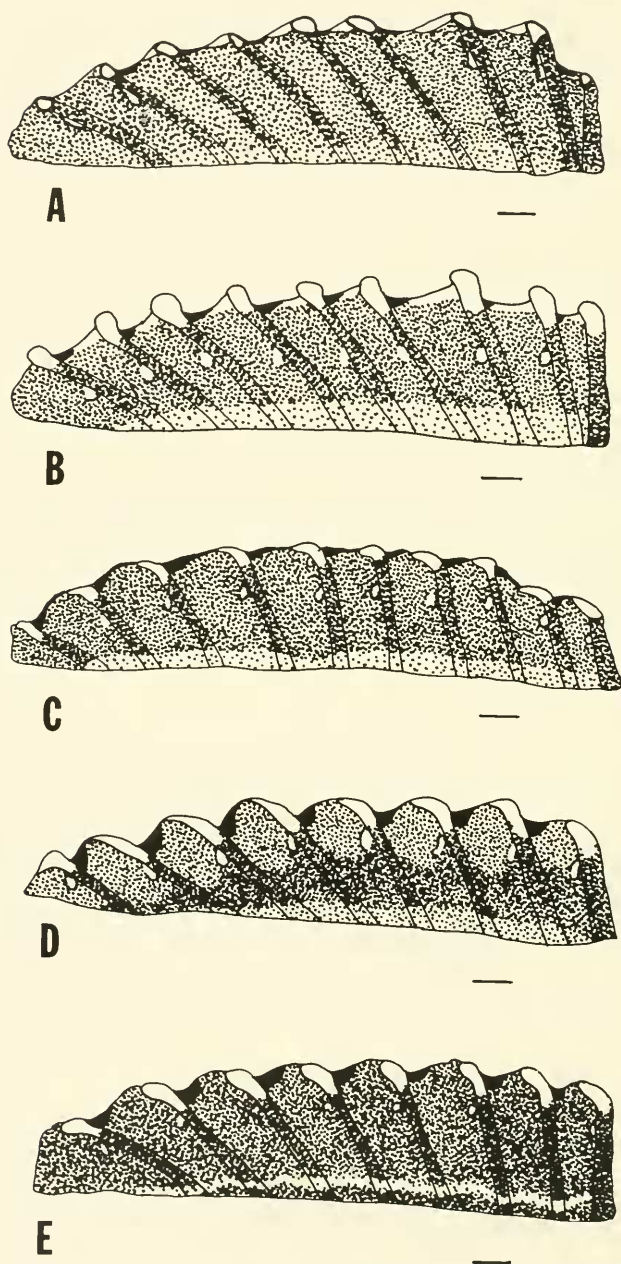


FIGURE 2. First dorsal fin pigment patterns of breeding males of species in the *Etheostoma squamiceps* species group. A) *E. squamiceps*, 68 mm SL (INHS 75747). B) *E. neopterum*, 64 mm SL (KU 20900). C) *E. olivaceum*, 61 mm SL (KU 14402). D) *E. crossopterum*, 70 mm SL (KU 20896). E) *E. nigripinne*, 57 mm SL (KU 20000). Horizontal bar equals 1 mm.

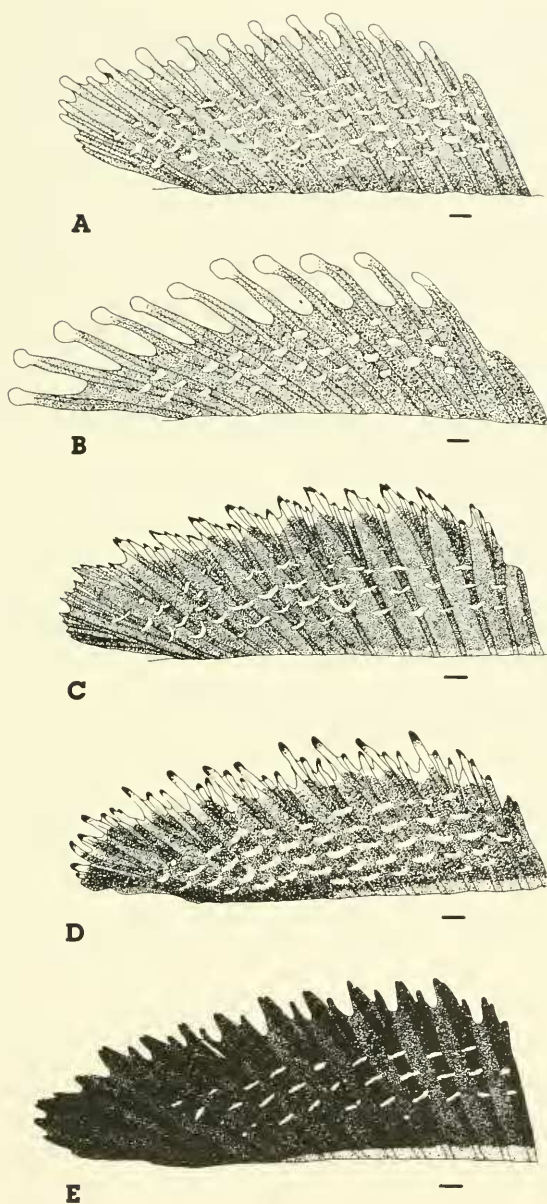


FIGURE 3. Second dorsal fin pigment patterns of breeding males of species in the *Etheostoma squamiceps* species group. A) *E. squamiceps*, 68 mm SL (INHS 75747). B) *E. neopterum*, 56 mm SL (KU 20762). C) *E. olivaceum*, 61 mm SL (KU 14402). D) *E. crossopteron*, 70 mm SL (KU 20896). E) *E. nigripinne*, 57 mm SL (KU 20000). Horizontal bar equals 1 mm.

USNM 1145 (erroneously given as USNM 1345 in original description). The second specimen, a female (USNM 197968) became paralectotype.

Etymology—The name *squamiceps* is taken from the Latin “squama” for scales and “iceps” for head in relation to the presence of scales on opercles and cheeks. The common name refers to the three dark spots at the base of the caudal fin.

Diagnosis—Dorsal fin rays with branches not adnate and possessing moderately large, fleshy knobs in breeding males; anal fin rays usually 7; pectoral fin rays usually 11; first dorsal fin without orange band.

Material examined—Lectotype: USNM 1145; Kentucky: Logan Co., Russellville. Paralectotype: USNM 197968; same locality data as lectotype.

Other specimens examined during the study are listed below in geographic order by drainage and river system:

Ohio R. Drainage: Cache R. System: Illinois: Union Co.: INHS 17833 (19), 17838 (9), 17847 (7), 18110 (1), 18033 (2); KU 7267 (6). Johnson Co.: INHS 2221 (1).

Tributaries Ohio R.: Illinois: Hardin Co.: INHS 985 (2), 994 (4), 999 (1), 1027 (6), 84986 (1), 85003 (1), 88504 (16); UMMZ 111641 (1), 171805 (3), 171806 (9); TU 22377 (2). Pope Co.: INHS 1480 (3), 1484 (4), 1560 (1), 1576 (6), 1593 (21), 86187 (3), 88503 (2); UL 9176 (2), 9182 (3), 9186 (1), 12871 (8). Kentucky: Crittenden Co.: INHS 78340 (3), 78356 (1), 78358 (1), 78376 (26), 78379 (2), 78392 (2). Livingston Co.: INHS 77707 (3), 78516 (7), 78534 (8).

Wabash R. System: Illinois: White Co.: UMMZ 102407 (4). Indiana: Posey Co.: INHS 75747 (12), 73680 (1), 73681 (1). Gibson Co.: UMMZ 65040 (4).

Tradewater R. System: Kentucky: Caldwell Co.: INHS 86756 (33); KU 14409 (1); MEB 110 (28); SIUC uncat. (10); UL 5114 (1). Crittenden Co.: INHS 77716 (1), 77720 (2), 77730 (3). Christian Co.: SIUC uncat. (1).

Lower Green R. System: Kentucky: Logan Co.: INHS 77734 (4). Christian Co.: INHS 27501 (9); KU 16223 (3); MEB 111 (1). Butler Co.: KU 16432 (3).

Upper Green R. System: Kentucky: Grayson Co.: INHS 75755 (3); UL 6280 (2), 7987 (4), 8677 (1). Adair Co.: KU 11565 (6), 14405 (4), 16428 (1). Larue Co.: KU 5816 (5); TU 19530 (3); UMMZ 154753 (1); UT 91.2607 (3). Hardin Co.: UL 5031 (2), 5983 (3), 7023 (3), 8665 (1), 11896 (3), 12904 (3). Green Co.: UMMZ 86472 (1).

Barren R. System: Kentucky: Allen Co.: INHS 75991 (4); KU 11642 (1); UL 6878 (1). Tennessee: Macon Co.: UMMZ 165382 (1). Clay Co.: INHS 82642 (7); UMMZ 165366 (4). Sumner Co.: MEB 107 (2), 108 (11).

Cumberland R. Drainage: Red R. System: Kentucky: Christian Co.: INHS 75792 (1); UL 5286 (1). Logan Co.: INHS 78556 (3), 75800 (4); UL 5833 (2), 6690 (1). Todd Co.: INHS 77744 (1), 77696 (25), UL 5323

(1). Tennessee: Montgomery Co.: UMMZ 160995 (1). Robertson Co.: MEB 112 (6), 184 (1).

Description—*Etheostoma squamiceps* is a large, robust *Catonotus*; largest specimen a male 72.5 mm SL. Males generally larger than females, largest female 58 mm SL. Infraorbital canal incomplete with narrow interruption below eye, pores normally 4-3 or 4-4; preoperculomandibular canal pores 10; supraorbital canal pores 4 or 5; supratemporal interrupted medially, pores 2-2; lateral canal pores 5; frenum narrow to moderate; branchiostegal rays 6 per side, membranes slightly to moderately joined; preopercle entire; genital papilla broad and flat, not bifurcated.

Cheeks, opercles, breast and nape normally scaled. Lateral line scales 41-60, 12-51 pored, unpored scales 5-35; transverse scale rows below lateral line 7-11 (usually 9), above lateral line 5-8 (6).

First dorsal fin with 7-11 (8-9) spines, fleshy knobs at tips present in both sexes; second dorsal rays 12-15 (13); anal spines 2, anal rays 6-9 (7-8); branched caudal rays 14-17; pectoral rays 10-12 (11).

Body proportions: HL/SL 0.27-0.33 ($\bar{X}$ = 0.29); BD/SL 0.17-0.26 (0.21); CPD/SL 0.08-0.16 (0.01); P_1 L/SL 0.19-0.26 (0.23); P_2 L/SL 0.16-0.24 (0.20); PreOL/HL 0.18-0.36 (0.25); EW/HL 0.17-0.31 (0.25); DFH/DFB 0.16-0.56 (0.31).

Coloration of freshly preserved specimens: General coloration of females and non-breeding males consists of irregular mottling of brown on a light tan background (Fig 1). Anterior lateral line pores unpigmented, forming pale line against dark mottling. Dark humeral spot large. Base of the caudal fin with three dark spots which may occasionally coalesce to form a vertical bar. Dorsum normally paler than sides, especially in specimens from the northern part of range where a sharply delineated wide pale band extends posteriorly from occiput to caudal peduncle. Pale dorsal area usually crossed by 8 (sometimes 9) dark bands. Venter normally unmarked except for spot at base of each pectoral fin. Head typically with pre-, post-, and suborbital dark bars. Cheeks usually mottled; may have a dark diagonal line from below the eye posterodorsally connecting with postorbital bar at the anterior edge of opercle.

Spinous dorsal fin colorless except for a few small melanophores forming indistinct subdistal and basal bands; base of fin thickened; membrane thickened at tip of spines, forming inconspicuous light colored knobs. Membranes of soft dorsal fin with clusters of melanophores forming 3-7 interrupted bands and rather indistinct basal band; base of fin thickened. Caudal fin with melanophores clustered along rays and forming 6-8 narrow dark bands. Anal and pelvic fins unpigmented; pectoral fins unpigmented to lightly barred with up to 9 narrow brown bands.

Breeding males dark. Sides uniformly dark brown or gray; caudal spots enlarged to form vertical bar; dorsum uniformly dark; head much darker, almost black, often obscuring regular markings; lower part of head greatly swollen; venter dark gray (Fig. 1). During actual courtship and egg care, strongly contrasting alternating dark and light bars develop on sides (Page, 1975b, p. 10 for photograph). First dorsal fin black except for large

pale yellow or white knobs on spines and occasional small, unpigmented vertical windows behind each spine; basal part of fin with narrow clear band and membrane thickened (Fig. 2). Second dorsal fin black with a broad distal white or pale yellow band and 4-6 rows of short, concave, pale dashes across rays; basal portion of fin thickened; at peak of breeding season tips of rays greatly elongated, terminating in round white or yellow knobs (Fig. 3). Anal fin dark with pale distal margin; membrane thickened around first spine. Pelvic fins dark except for paler membrane around spine and pale distal margin. Caudal and pectoral fins unchanged from non-breeding coloration. Genital papilla darkly pigmented.

Distribution—*Etheostoma squamiceps* is widespread, but not common, in the Green drainage and Red river system of the Cumberland drainage in Kentucky and Tennessee. It occurs more abundantly in Tradewater River and nearby direct tributaries of Ohio River in Kentucky and southern Illinois. Isolated populations occur in tributaries of Wabash River in Gibson and Posey counties, Indiana, and White County, Illinois, and in Cache River in southwestern Illinois (Fig. 4). Specimens from Kaskaskia River, Shelby County, Illinois, reported in Forbes and Richardson (1908:313) have been reidentified as *Etheostoma asprigene* (pers. obs.).

Variation—*Etheostoma squamiceps* shows little sexual dimorphism except for size and pigmentation. Males have a deeper caudal peduncle, smaller eye, and more pored lateral-line scales ($\alpha = .001$) than do females (Table 1). Ontogenetic variation is more pronounced. Small specimens (<40 mm SL) have a larger eye; longer pelvic fins; higher spinous dorsal fins; fewer pored lateral-line scales; more unpored lateral-line scales

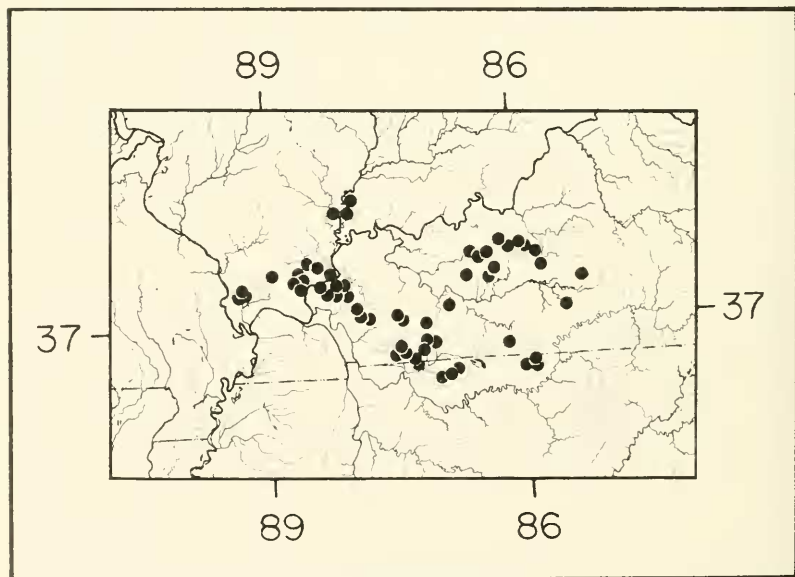


FIGURE 4. Distribution of *Etheostoma squamiceps*.

($\alpha = .001$); longer heads, and thinner caudal peduncles ($\alpha = .05$) than do larger individuals (Table 2).

To evaluate geographic variation, the range of *E. squamiceps* was divided into eight operational units. The Green River system was divided into three areas: Barren River, Upper Green (eastern headwaters plus Nolin and Rough rivers), and lower Green (Mud and Pond rivers). Other populations include Red River, Cache River, Wabash River, Tradewater River, and small direct tributaries of Ohio River in southeastern Illinois and northwestern Kentucky. Because of small sample size, the lower Green and Barren populations were not used in analyzing proportions.

Geographic variation in pigmentation, squamation, meristics and morphometrics is extensive between populations of *E. squamiceps*.

Pigmentation: Dorsal pigmentation varies individually and geographically. Individuals from the Red river system have a narrow, light tan dorsal band extending from nape area to caudal peduncle, which is crossed by several dark cross bars. Populations in northern and western parts of the range have reduced pigmentation and often have a wide pale dorsal band which may even extend down onto the sides. Dorsal cross bars may be reduced to a scalloping effect on the dorsal stripe.

Squamation: Of areas of the body exhibiting variation in squamation, the peripheral populations (Cache, Ohio, Wabash, Barren rivers) show reduced squamation on nape, opercles, and cheeks (Table 3; Figs. 5-7).

Meristics and morphometrics: Dorsal spines, dorsal rays, anal rays, pectoral rays, lateral-line scales, pored lateral-line scales, unpored lateral-

TABLE 1. Morphological characters exhibiting sexual dimorphism in species of the *Etheostoma squamiceps* species group. Means and ranges of proportions in thousands of a millimeter.

Species & Character	N	MALES			N	FEMALES		
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD
<i>Etheostoma squamiceps</i>								
Pored Lateral Scales	48	29-51	38.5	5.46	34	24-47	35.8	5.78
EW/HL	49	171-318	243	0.03	34	192-308	268	0.03
CPD/SL	51	112-147	131	0.01	40	109-167	125	0.01
<i>Etheostoma neopterum</i>								
P2L/SL	22	167-224	201	0.01	25	171-217	193	0.01
CPD/SL	22	105-158	128	0.02	25	111-138	120	0.01
<i>Etheostoma crossopterum</i>								
Pored Lateral Scales	24	22-44	35.2	5.17	36	7-39	29.2	7.01
Unpored Lateral Scales	24	9-28	18.4	6.31	36	12-37	24.5	6.67
CPD/SL	23	111-142	128	0.01	36	92-133	188	0.01
EW/HL	23	186-292	239	0.03	36	211-318	268	0.03
PreOL/SL	23	222-294	261	0.02	36	167-304	246	0.03
P1L/SL	23	190-258	231	0.01	36	207-269	237	0.01
<i>Etheostoma nigripinne</i>								
CPD/SL	46	116-159	137	0.01	24	96-154	129	0.14
EW/HL	46	188-308	253	0.03	24	222-300	268	0.02

line scales, transverse scale rows above and below lateral line, HL/SL, BD/SL, P₁L/SL, P₂L/SL, PreOL/HL, EW/HL, and DFH/DFB all varied significantly geographically ($\alpha = 0.001$) (Tables 4-11).

Peripheral populations from Cache, Tradewater, and Red rivers are most extreme in variation. Anal rays generally 7 except in the Tradewater, Barren, and Red rivers which typically have 8 rays (Table 7). Scales above lateral line generally 8 except in populations from the Tradewater, lower Green, and Barren rivers and to a lesser extent, the Red River which most commonly have 9 rows (Table 10). Scales below lateral line generally 6 except in Wabash River populations which average more (Table 11). Specimens from the Cache River have fewer dorsal rays and spines, and to a lesser extent, populations from Red River, upper Green River, and small tributaries of the Ohio River show some reduction in the number of dorsal spines (Tables 5 and 6).

Habitat and Life History—The preferred habitat of *E. squamiceps* is small, quiet streams with either large, flat rocks or with bedrock bottom where they hide in crevices and under ledges. In this type of habitat *E.*

TABLE 2. Characters exhibiting ontogenetic variation in species of the *Etheostoma squamiceps* group. Means and ranges of proportions in thousands of a millimeter.

Species & Character	N	< 40 mm SL			N	> 40 mm SL		
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD
<i>Etheostoma squamiceps</i>								
Pored Lateral Scales	28	12-42	28.7	7.59	82	24-51	36.9	6.92
Unpored Lateral Scales	28	10-31	21.0	6.31	82	5-28	13.7	4.97
CPD/SL	27	98-161	123	0.02	91	109-167	128	0.01
EW/HL	28	235-333	282	0.03	82	171-318	253	0.03
DFH/DFB	27	278-538	388	0.03	83	206-550	324	0.04
<i>Etheostoma neopterum</i>								
Pored Lateral Scales	59	14-41	34.1	4.81	47	9-42	36.6	3.56
Unpored Lateral Scales	59	9-31	14.8	4.16	47	7-23	13.1	3.45
HL/SL	59	282-356	313	0.01	47	237-330	301	0.02
CPD/SL	59	102-154	127	0.01	47	111-158	124	0.01
EW/HL	59	250-353	292	0.01	47	214-320	265	0.01
BD/SL	59	189-228	206	0.01	47	173-219	197	0.02
DFH/DFB	59	286-500	382	0.01	47	265-615	334	0.01
<i>Etheostoma crossopterum</i>								
Pored Lateral Scales	55	7-43	23.9	8.28	60	7-44	31.6	6.98
Unpored Lateral Scales	55	15-42	29.6	7.67	60	9-37	22.1	7.17
HL/SL	57	284-350	306	0.01	59	267-321	297	0.01
EW/HL	57	227-333	289	0.02	59	186-318	257	0.03
DFH/DFB	57	222-538	356	0.05	59	200-588	306	0.07
P1L/SL	57	203-269	242	0.02	59	190-269	234	0.01
P2L/SL	57	176-242	209	0.01	59	165-248	199	0.02
<i>Etheostoma nigripinne</i>								
HL/SL	30	278-328	297	0.01	70	264-318	291	0.01
EW/HL	30	250-333	280	0.02	70	188-308	258	0.03
DFH/DFB	30	211-500	339	0.06	70	174-381	280	0.05
P2L/SL	30	179-233	208	0.01	70	161-233	201	0.02

squamiceps may be abundant. Although they usually avoid riffles they may occasionally be found in quiet riffles in late summer when pools are too low to provide cover. They tend to avoid fast, gravelly streams and are very rare over sand or mud substrate. Darter species most commonly associated with *E. squamiceps* are *Etheostoma barbouri* in the eastern portion of its range and *E. kennicotti* to the west. Other fishes commonly found with *E. squamiceps* are *Camptostoma anomalum*, *Pimephales notatus*, *Semotilus atromaculatus*, *Phoxinus erythrogaster*, *Fundulus olivaceus*, and *Lepomis cyanellus*.

Page (1974) gave detailed information on reproduction, growth, food,

TABLE 3. Squamation of nape, cheek, and opercular regions in species of the *Etheostoma squamiceps* species group. N=naked, E=embedded and S=exposed.

Species & Population	N	Nape			Cheek			Opercle		
		N	E	S	N	E	S	N	E	S
<i>Etheostoma squamiceps</i>										
Cache River	34	0	32	2	16	18	0	0	32	2
tribs., Ohio River	35	0	35	0	0	35	0	0	35	0
Wabash River	14	0	13	1	0	12	2	0	13	1
Tradewater River	35	0	6	29	0	33	2	0	6	29
Lower Green River	14	0	10	4	2	12	0	0	10	4
Upper Green River	25	0	21	4	6	17	2	0	21	4
Barren River	14	0	13	1	0	14	0	0	13	1
Red River	42	0	36	6	0	39	3	0	36	6
TOTALS	213	0	166	47	24	180	9	0	166	47
<i>Etheostoma neopterum</i>										
Clarks River	55	0	37	18	0	55	0	0	19	36
Big Sandy River	51	1	49	1	1	49	1	0	42	9
Duck River	23	0	23	0	0	23	0	0	23	0
Shoal Creek	26	0	16	10	5	15	6	0	14	12
TOTALS	155	1	125	29	6	142	7	0	98	57
<i>Etheostoma crossopterygion</i>										
Lower Cumberland River	46	0	46	0	20	26	0	0	43	3
Middle Cumberland River	58	0	57	1	20	38	0	0	55	3
tribs., Mississippi River	11	3	8	0	11	0	0	3	8	0
Duck River	48	0	43	5	22	26	0	0	45	3
Cypress Creek	42	0	31	11	0	42	0	0	17	25
TOTALS	205	3	185	17	73	132	0	3	168	34
<i>Etheostoma nigripinne</i>										
western tribs.,										
Tennessee River	37	0	32	5	0	37	0	0	32	5
eastern tribs.,										
Tennessee River	24	0	24	0	0	24	0	0	21	3
southern tribs.,										
Tennessee River	64	0	53	11	0	63	1	0	53	11
Shoal Creek	31	0	27	4	2	29	0	0	25	6
Elk River	44	0	43	1	1	43	0	1	38	5
TOTALS	200	0	179	21	3	196	1	1	169	30
<i>Etheostoma olivaceum</i>										
Caney Fork River	100	0	61	39	100	0	0	100	0	0

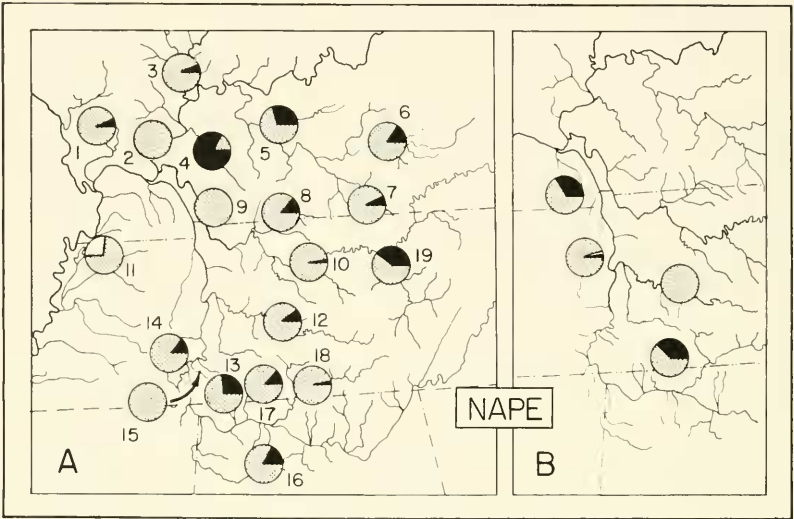


FIGURE 5. Squamation of nape of species in the *Etheostoma squamiceps* species group. Each circle represents a river system identified in Table 3. In each circle stippled areas represent embedded scales, solid black areas exposed scales, and white areas naked. Frequencies of each condition are given in Table 3. Numbers refer to populations as outlined below. Area A includes *E. squamiceps*, *E. olivaceum*, *E. crossopterum*, and *E. nigripinne*. Area B is *E. neopterum*. Within area A, *E. squamiceps* = 1-8, *E. crossopterum* = 9-13, *E. nigripinne* = 14-18, and *E. olivaceum* = 19.

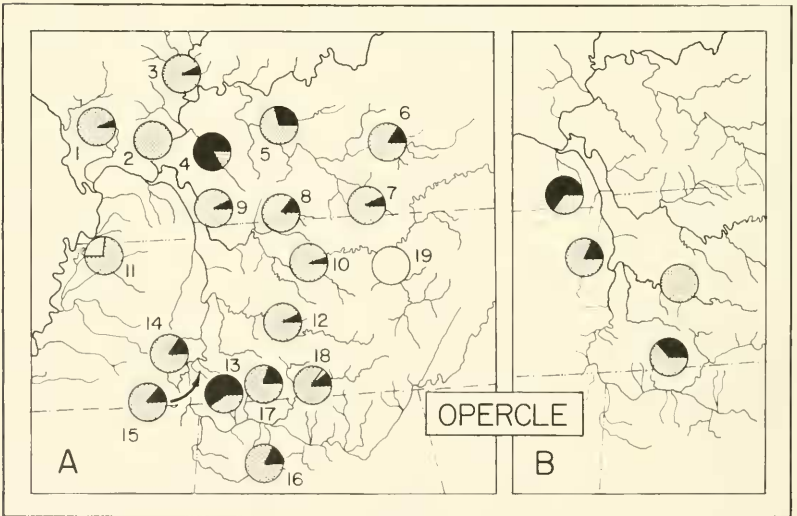


FIGURE 6. Squamation of opercles in the *Etheostoma squamiceps* species group. Area A includes *E. squamiceps*, *E. crossopterum*, *E. nigripinne*, and *E. olivaceum*. Area B includes *E. neopterum*. See Figure 5 and Table 3 for explanation of numbers and color codes.

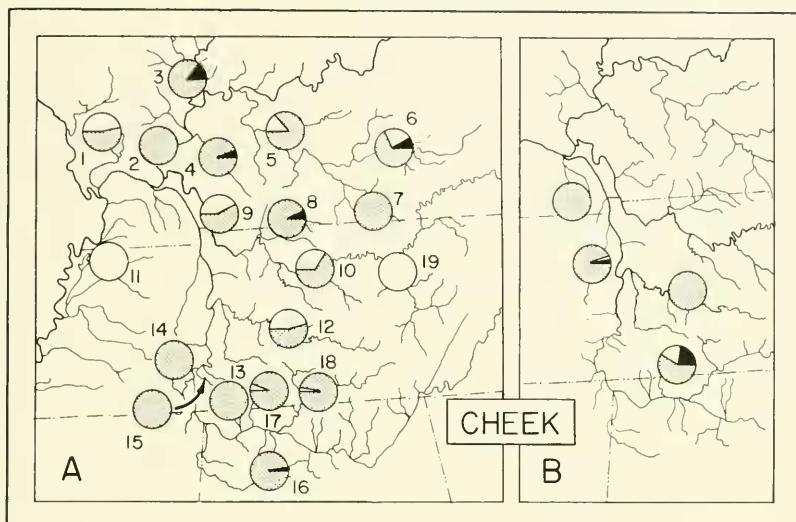


FIGURE 7. Squamation of cheek regions in the *Etheostoma squamiceps* species group. Area A includes *E. squamiceps*, *E. crossopterum*, *E. nigripinne* and *E. olivaceum*. Area B includes *E. neopterum*. See Figure 5 and Table 3 for explanation of numbers and color codes.

habitats, population composition, predation, and parasitism of this species. This life history study was actually a composite of *E. squamiceps* (Big Creek) and a heretofore undescribed species from the Cumberland River system (Richland Creek). Life history data from this study, however, are separable since data on these two species were presented separately and ecological comparisons were made.

Etheostoma crossopterum NEW SPECIES

Fringed Darter

Figs. 2, 3, 8, 10.

Holotype—University of Kansas, KU 20896, breeding male 69.8 mm SL (Fig. 8), collected from McKnight Branch, 8 km N Readyville, Rutherford County, Tennessee, 2 April 1980, Marvin E. Braasch.

Paratypes—A total of 85 specimens deposited as follows: 5—University of Kansas (KU 20897, 46.6–75.6 mm SL, same data as holotype); 26—Illinois Natural History Survey (INHS 74918, 29.0–57.0 mm SL, East Fork Stones River at Lofton, Rutherford Co., TN, 14 March 1976); 11—University of Michigan Museum of Zoology (UMMZ 174481, 31.6–53.4 mm SL, Richland Creek on N edge of Belle Meade, SSW Nashville, Davidson Co., TN, 2 May 1954); 4—United States National Museum (USNM 266733, 40.0–47.2 mm SL, same data as UMMZ 174481); 27—UMMZ 177570 (15.0–59.5 mm SL, Richland Creek at Leake Ave., off US 70S, SW Nashville, Davidson Co., TN, 16 May 1956); 4—Southern Illinois University at Carbondale (SIUC 9782, 46.6–59.4 mm SL, same data as UMMZ 177570); 4—University of Tennessee (UT 91.838,

TABLE 4. Geographically variable body proportions in *Etheostoma squamiceps*. Measurements and means in hundredths of a millimeter.

Population	N	HL/SL			PreOL/HL			EW/HL			BD/SL		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Cache River small tribs., Ohio River	24	29-33	30	0.01	24-32	27	0.03	17-29	23	0.03	20-23	21	0.008
Wabash River	31	28-31	29	0.02	19-36	24	0.03	21-32	26	0.03	17-22	19	0.01
Tradewater River	13	28-33	30	0.02	18-32	26	0.04	20-31	21	0.02	19-24	22	0.01
Upper Green River	23	27-30	29	0.01	19-29	23	0.02	20-31	27	0.03	19-26	22	0.01
Red River	10	28-31	29	0.01	23-28	23	0.02	21-28	25	0.02	18-23	21	0.02
	28	27-31	29	0.01	22-29	26	0.02	23-30	27	0.02	20-25	22	0.01
TOTALS	129	27-33	29	0.01	18-36	25	0.02	17-32	25	0.03	17-26	21	0.01

Population	N	P ₁ L/SL			P ₂ L/SL			DFH/DFB		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Cache River small tribs., Ohio River	24	21-26	24	0.01	19-22	20	0.01	27-42	33	0.04
Wabash River	31	19-25	22	0.02	17-21	19	0.01	24-56	34	0.06
Tradewater River	13	19-25	23	0.02	19-24	20	0.02	27-42	33	0.03
Upper Green River	23	19-26	22	0.02	17-21	19	0.01	16-35	26	0.05
Red River	10	20-24	22	0.01	17-22	19	0.01	27-36	31	0.03
	28	21-26	24	0.01	18-22	20	0.01	21-45	30	0.05
TOTALS	129	19-26	23	0.02	16-24	19	0.01	16-56	31	0.05

56.6-75.5 mm SL, Stones Creek at gravel road just off I-40 (Mt. Juliet exit), Wilson Co., TN, 12 May 1973); 3—UT 91.822 (48.8-73.0 mm SL, same data as UT 91.838); 2—University of Alabama Ichthyological Collection (UAIC 7713.01, 63.5-64.0 mm SL, same data as UT 91.838); 2—Tulane University (TU 139109, 59.4-64.7 mm SL, same data as UT 91.838).

Etymology—The name *crossopterus* is taken from the Greek "crosso" meaning fringed or tassled and "pteron" for fin, in reference to the morphology of the distal border of the second dorsal fin of breeding males. The common name also refers to this character.

Diagnosis—Distal margin of second dorsal fin in breeding males with broad light band, rays extending far beyond membrane margin, tipped in black, and lacking fleshy knobs. Infraorbital canal incomplete. Anal fin rays usually 7.

TABLE 5. Counts of dorsal fin spines in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Dorsal Spines					N	$\bar{X}$	SD
	7	8	9	10	11			
<i>Etheostoma squamiceps</i>								
Cache River	1	21	12			34	8.3	0.52
small tribs., Ohio River		10	24		1	35	8.7	0.59
Wabash River		5	9			14	8.6	0.47
Tradewater River		5	21	9		35	9.1	0.62
Lower Green River		2	12			14	8.8	0.35
Upper Green River		11	12	2		25	8.6	0.62
Barren River		1	11	2		14	9.0	0.45
Red River	1	15	25	1		42	8.6	0.57
TOTALS	2	70	126	14	1	213	8.7	0.57
<i>Etheostoma neopterum</i>								
Clarks River		1	51	3		55	9.0	0.26
Big Sandy River		13	34	4		51	8.8	0.55
Duck River		14	6			20	8.3	0.45
Shoal Creek		7	17	2		26	8.8	0.56
TOTALS		35	108	9		152	8.7	0.46
<i>Etheostoma crossopterus</i>								
Lower Cumberland River		22	40	4		66	8.7	0.56
Middle Cumberland River		18	38	2		58	8.7	0.51
direct tribs., Mississippi River		8	4			12	8.3	0.47
Duck River		25	25			50	8.5	0.50
Cypress Creek			27	6		33	9.1	0.38
TOTALS		73	134	12		219	8.7	0.56
<i>Etheostoma nigripinne</i>								
western tribs., Tennessee River	1	25	10	1		37	8.3	0.56
eastern tribs., Tennessee River	1	18	11			30	8.3	0.53
southern tribs., Tennessee River	2	37	8	3		50	8.2	0.61
Shoal Creek		21	5			26	8.1	0.39
Elk River	3	27	18	2		50	8.3	0.66
TOTALS	7	128	52	6		193	8.3	0.59
<i>Etheostoma olivaceum</i>								
Caney Fork River		7	43	7		57	9.2	0.45

Material examined—Specimens examined during this study, but not designated as types are arranged below by drainage and river system.

Mississippi R. Dr.: Tennessee, Obion Co.: INHS 27557 (3); KU 20925 (7), UT 91.189 (1), 91.166 (9), 91.1713 (7), 91.998 (10).

Tennessee R. Dr.: Duck R. System: Tennessee, Bedford Co.: INHS 77517 (5), 79364 (11), 76948 (14), 76137 (3); KU 20898 (1), 20946 (10), 20949 (28), 20959 (10); UMMZ 121038 (2), 121052 (6), 121094 (1), 121107 (1), 121113 (2), 121122 (1), 121137 (13), 121148 (1), 121184 (3), 121194 (18), 121252 (2), 121270 (11), 121260 (1), 121282 (6), 121294 (1), 121338 (1), 121351 (1); UT 91.746 (17), 91.768 (21), 91.774 (11), 91.1603 (4), 91.1478 (27); UAIC 2534 (1), 2535 (1), 2698 (2); MEB 114 (2), 115 (1), 116 (1), 117 (1), 118 (1). Marshall Co.: INHS 86781 (32); KU 14193 (1), 16221 (31); UAIC 2858 (23); UMMZ 121389 (5), 121453 (2), 121479 (2); UT 91.1293 (2), 91.1294 (1). Maury Co.: INHS 27582

TABLE 6. Counts of dorsal fin rays in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Dorsal Fin Rays						N	$\bar{X}$	SD
	10	11	12	13	14	15			
<i>Etheostoma squamiceps</i>									
Cache River			16	15	3		34	12.6	0.64
small tribs., Ohio River			7	26	2		35	12.8	0.48
Wabash River			5	7	2		14	12.8	0.67
Tradewater River			4	23	8		35	13.1	0.57
Lower Green River			3	7	4		14	13.0	0.70
Upper Green River			3	18	4		25	13.0	0.52
Barren River			4	5	4	1	14	13.1	0.91
Red River			6	20	16		42	13.2	0.68
TOTALS			48	121	43	1	213	12.9	0.64
<i>Etheostoma neopterum</i>									
Clarks River		3	22	24	6		55	12.6	0.75
Big Sandy River	4	42	3	1	1		51	11.0	0.62
Duck River		2	17	1			20	11.9	0.38
Shoal Creek	1	12	13				26	11.5	0.58
TOTALS	5	59	55	26	7		152	11.8	0.58
<i>Etheostoma crossopterum</i>									
Lower Cumberland River		2	25	37	2		66	12.5	0.60
Middle Cumberland River		2	31	24	1		58	12.4	0.58
direct tribs., Mississippi River		1	6	5			12	12.3	0.62
Duck River			8	23	19		50	13.2	0.70
Cypress Creek				6	23	4	33	13.9	0.54
TOTALS		5	70	95	45	4	219	12.8	0.62
<i>Etheostoma nigripinne</i>									
western tribs., Tennessee River		1	4	21	11		37	13.1	0.70
eastern tribs., Tennessee River			1	14	14	1	30	13.5	0.61
southern tribs., Tennessee River			3	28	16	3	50	13.3	0.69
Shoal Creek			1	17	7	1	26	13.3	0.60
Elk River		1	13	26	10		50	12.9	0.72
TOTALS		2	22	106	58	5	193	13.2	0.69
<i>Etheostoma olivaceum</i>									
Caney Fork River		4	60	35	1		100	12.3	0.57

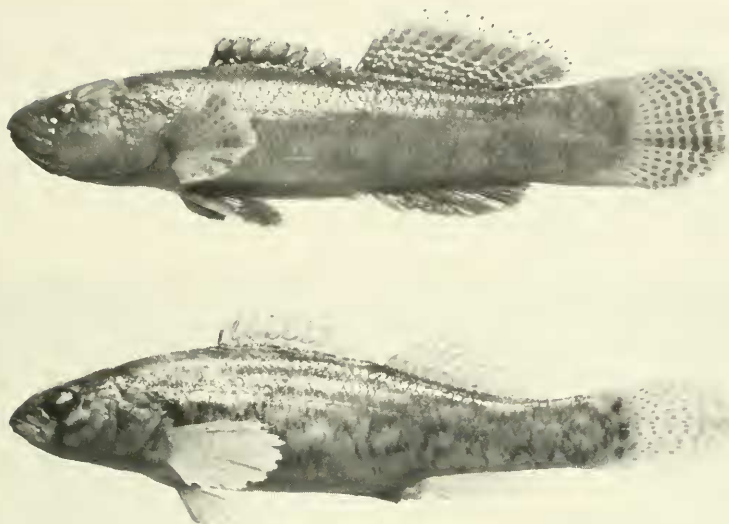


FIGURE 8. *Etheostoma crossopterygum*, new species. Top, Holotype, male 69.8 mm SL (KU 20896); Bottom, Paratype, female, 49.8 mm SL (KU 20897).

(15), 79338 (1); KU 10674 (13), 10691 (1), 20929 (40); UMMZ 104685 (3), 104695 (1), 104706 (2), 104720 (1), 104746 (1), 104798 (1), 105077 (5), 121514 (2), 121559 (5), 121598 (1), 121605 (1), 121608 (1); UT 91.745 (1), 91.764 (2); MEB 200 (12), 202 (2), 203 (1). Williamson Co.: UMMZ 104776 (6), 121546 (4), 121566 (1), 121577 (5). Coffee Co.: INHS 75761 (5); KU 20933 (1); UAIC 2418 (1); UMMZ 120841 (1), 120877 (7), 120889 (21), 120896 (7), 120906 (22), 120916 (1), 120926 (3), 120972 (9); UAIC 2418 (1); UT 91.627 (12), 91.714 (26), 91.715 (30), 91.1445 (8). Hickman Co.: INHS 77817 (4), 77636 (6), 77644 (4); UMMZ 104757 (3), 104820 (1), 104974 (1), 105284 (5); MEB 97 (20). Lawrence Co.: INHS 79312 (1); UMMZ 105123 (3), 105150 (4), 105169 (1); UT 91.99 (1); MEB 204 (2). Perry Co.: INHS 77661 (1); KU 10671 (5); UMMZ 105250 (2); TU 14694 (1); MEB 120 (2). Lewis Co.: KU 20852 (1); UMMZ 105109 (2); MEB 96 (3), 201 (5). Wayne Co.: INHS 86751 (14); KU 20899 (2); UMMZ 105180 (3), 113945 (2); MEB 122 (4), 123 (6), 205 (1), 206 (1). Humphreys Co.: INHS 77836 (10); UMMZ 104945 (2). Dickson Co.: UMMZ 104852 (1), 104881 (1).

Cypress Creek System: Tennessee: Wayne Co.: INHS 83082 (2); MEB 100 (16). Alabama: Lauderdale Co.: INHS 76130 (17), 86778 (5); UAIC 1589.11 (6), 1991.02 (2), 2509.05 (1), 3204.12 (23), 3205.05 (7), 3206.10 (16), 3207.10 (3), 3208.11 (10), 3238.08 (5), 3239.09 (14), 3240.12 (51), 3241.06 (1), 3242.09 (49), 3243.11 (40), 3520.09 (3).

Middle Cumberland R. Dr.: Tennessee: Rutherford Co.: INHS 83090 (3), 74918 (26), 86760 (6), 86763 (1); KU 11477 (8); SIUC uncat.

(16); UMMZ 158764 (5). Cannon Co.: INHS 75873 (2), 86780 (3); KU 11681 (1), 20944 (8); UT 91.1537 (1). Williamson Co.: INHS 75870 (1), 83122 (5), 75870 (1); MEB 124 (1); UMMZ 177581 (23). Dickson Co.: KU 14196 (2); TU 14663 (1). Davidson Co.: INHS 27463 (9), 75712 (11); MEB 125 (1); UMMZ 96363 (53), 96371 (4), 174481 (15), 177570 (31); UT 91.1297 (2), 91.1316 (4). Smith Co.: KU 12012 (5); MEB 126 (1). Montgomery Co.: INHS 82996 (5), 83007 (3), 75766 (2); MEB 10 (1); UMMZ 160995 (1). Sumner Co.: MEB 127 (11); UAIC 2974 (9); UMMZ 16402 (2). Cheatham Co.: INHS 82588 (1), 82596 (5), 88501 (1); UT 91.207 (4). Rutherford Co.: INHS 83085 (4). Trousdale Co.: INHS 83040 (1); MEB 129 (1), 130 (1); SIUC uncat. (5). Wilson Co.: KU 20938 (3); MEB 132 (17), 133 (7); UT 91.165 (83), 91.822 (8), 91.838 (4), 91.1085 (4). Cannon Co.: UT 91.1537 (1).

TABLE 7. Counts of anal fin rays in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Fin Rays				N	$\bar{X}$	SD
	6	7	8	9			
<i>Etheostoma squamiceps</i>							
Cache River	1	27	5	1	34	7.2	0.15
small tribs., Ohio River	4	15	15	1	35	7.4	0.72
Wabash River	1	12	1		14	7.0	0.63
Tradewater River	1	11	21	2	35	7.7	0.63
Lower Green River	2	5	7		14	7.4	0.72
Upper Green River	3	14	7	1	25	7.2	0.71
Barren River		5	6	3	14	7.9	0.74
Red River	1	12	26	3	42	7.7	0.62
TOTALS	13	101	88	11	213	7.5	0.65
<i>Etheostoma neopterum</i>							
Clarks River	1	15	29	10	55	7.9	0.72
Big Sandy River	2	26	22	1	51	7.5	0.60
Duck River			19	1	20	8.1	0.22
Shoal Creek	1	21	4		26	7.1	0.43
TOTALS	4	62	74	12	152	7.7	0.49
<i>Etheostoma crossopternum</i>							
Lower Cumberland River	3	35	27	1	66	7.4	0.60
Middle Cumberland River	6	38	14		58	7.1	0.57
direct tribs., Mississippi River	2	7	2	1	12	7.2	0.79
Duck River	1	15	33	1	50	7.7	0.55
Cypress Creek		19	13	1	33	7.5	0.55
TOTALS	12	114	89	4	219	7.4	0.59
<i>Etheostoma nigripinne</i>							
western tribs., Tennessee River	1	14	19	3	37	7.6	0.66
eastern tribs., Tennessee River		8	22		30	7.7	0.44
southern tribs., Tennessee River		21	28	1	50	7.6	0.53
Shoal Creek		12	14		26	7.5	0.50
Elk River	1	31	18		50	7.3	0.51
TOTALS	2	86	101	4	193	7.6	0.55
<i>Etheostoma olivaceum</i>							
Caney Fork River		40	15		55	7.3	0.45

Caney Fork R. System: Tennessee: Coffee Co.: UAIC 2417 (1), 2536 (1). Cannon Co.: INHS 82553 (1). Warren Co.: UT 91.646 (1).

Lower Cumberland R. Dr.: Kentucky: Lyon Co.: INHS 75877 (12); KU 11581 (1); UMMZ 174973 (7). Trigg Co.: KU 10722 (1). Caldwell Co.: INHS 75740 (3); UL 5080 (2), 6478 (2); UMMZ 174869 (7). Livingston Co.: INHS 78519 (26), 75863 (14), 75874 (12), 75875 (23), 75876 (1), 79367 (7); MEB 134 (23). Christian Co.: INHS 77702 (9); UL 10780 (29); UMMZ 154770 (5). Tennessee: Houston Co.: INHS 75814 (1). Stewart Co.: INHS 83122 (2), 77739 (3); UMMZ 161005 (8), 168371 (1).

Description—*Etheostoma crossopteron* is a large, robust *Catonotus*; largest specimen a male 83.5 mm SL. Males generally larger than females, largest female 61 mm SL. Infraorbital canal incomplete with narrow interruption below eye, pores normally 4-3, occasionally 4-4; preoperc-

TABLE 8. Counts of pectoral fin rays in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Pectoral Fin Rays				N	$\bar{X}$	SD
	10	11	12	13			
<i>Etheostoma squamiceps</i>							
Cache River	2	32			34	10.9	0.24
small tribs., Ohio River	4	29	2		35	10.9	0.41
Wabash River	2	12			14	10.9	0.35
Tradewater River	2	27	6		35	11.1	0.46
Lower Green River		11	3		14	11.2	0.41
Upper Green River	1	23	1		25	11.0	0.28
Barren River		14			14	11.0	0.00
Red River	7	35			42	10.8	0.37
TOTALS	18	183	12		213	11.0	0.36
<i>Etheostoma neopteron</i>							
Clarks River		16	37	2	55	11.7	0.51
Big Sandy River		4	43	4	51	12.0	0.40
Duck River		3	16	1	20	11.9	0.44
Shoal Creek		1	22	3	26	12.1	0.39
TOTALS		24	118	10	152	11.9	0.44
<i>Etheostoma crossopteron</i>							
Lower Cumberland River	2	50	14		66	11.2	0.46
Middle Cumberland River	11	46	1		58	10.8	0.42
direct tribs., Mississippi River	2	8	2		12	11.0	0.58
Duck River	1	29	20		50	11.4	0.53
Cypress Creek		4	21	8	33	12.1	0.59
TOTALS	16	137	58	8	219	11.3	0.49
<i>Etheostoma nigripinne</i>							
western tribs., Tennessee River	5	30	2		37	10.9	0.43
eastern tribs., Tennessee River		13	17		30	11.6	0.50
southern tribs., Tennessee River		19	30	1	50	11.6	0.52
Shoal Creek		23	3		26	11.1	0.32
Elk River	1	36	13		50	11.2	0.47
TOTALS	6	121	65	1	193	11.3	0.47
<i>Etheostoma olivaceum</i>							
Caney Fork River		4	84	12	100	12.1	0.39

TABLE 9. Counts of total, pored, and unpored lateral body scales in some species of the *Etheostoma squamiceps* species group.

Species & Population	N	Total			Pored			Unpored		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
<i>Etheostoma squamiceps</i>										
Cache River	34	49-58	53.2	2.33	25-43	36.2	4.48	10-29	17.0	4.56
small trib., Ohio River	35	44-56	51.4	2.62	21-51	40.3	6.05	5-28	11.1	5.31
Wabash River	14	42-54	50.6	3.56	33-43	38.6	2.38	8-19	12.9	2.80
Tradewater River	35	45-58	51.2	2.64	26-44	36.3	4.16	10-22	14.9	3.63
Lower Green River	14	45-54	50.4	2.92	16-43	30.6	7.64	11-32	19.1	6.68
Upper Green River	25	43-54	48.5	2.68	17-43	29.5	7.63	7-35	19.4	7.43
Barren River	14	43-60	50.7	4.82	21-42	30.1	5.53	13-35	20.6	5.89
Red River	42	41-56	48.1	2.81	12-44	30.5	7.10	9-31	17.6	6.51
TOTALS	213	41-60	50.5	2.95	12-51	34.1	6.03	5-35	16.2	5.65
<i>Etheostoma neopterum</i>										
Clarks River	55	44-55	49.5	2.46	22-45	35.5	4.60	7-29	14.1	4.30
Big Sandy River	51	45-55	49.1	2.37	14-41	34.9	4.33	8-31	14.1	3.55
Duck River	20	43-52	46.8	2.23	15-34	22.4	5.44	14-33	24.4	5.03
Shoal Creek	26	35-51	46.8	3.69	21-37	30.9	3.93	10-24	16.7	3.63
TOTALS	152	35-55	48.0	2.68	14-45	30.9	4.58	7-33	17.3	4.13
<i>Etheostoma crossopetrum</i>										
Lower Cumberland River	66	47-60	54.0	2.56	15-44	29.7	6.97	9-42	24.4	6.92
Middle Cumberland River	58	38-58	52.9	3.23	7-43	26.5	8.25	10-44	26.3	7.65
tribs., Mississippi River	12	44-61	53.6	3.97	20-44	30.3	6.39	8-36	23.7	8.38
Duck River	50	46-64	52.6	3.21	7-43	25.2	9.50	11-46	27.3	9.53
Cypress Creek	33	43-55	49.3	3.58	26-44	34.2	4.81	8-25	14.4	4.15
TOTALS	219	38-64	52.7	3.18	7-44	28.5	7.77	8-46	24.0	7.64
<i>Etheostoma nigriripine</i>										
western tribs., Tennessee River	36	42-54	47.9	2.44	10-39	24.6	5.88	15-35	23.2	4.86
eastern tribs., Tennessee River	30	43-52	47.2	2.09	14-37	28.4	5.42	11-35	18.8	5.28
southern tribs., Tennessee River	50	43-58	48.4	3.30	17-42	32.0	6.47	6-30	16.4	6.46
Shoal Creek	26	43-50	46.5	1.89	13-39	27.4	5.41	11-34	19.2	5.26
Elk River	50	43-55	49.6	2.53	15-45	26.0	6.07	7-35	23.6	6.47
TOTALS	193	42-58	48.2	2.64	10-45	27.8	6.04	6-35	20.3	5.94

culomandibular canal pores 10; supraorbital canal pores 4 or 5; supratemporal canal interrupted medially, pores 2-2; lateral canal pores 5; frenum narrow to moderate; branchiostegal rays six, membranes slightly to moderately joined; preopercle entire. Genital papilla of females broad, flat, and darkly pigmented.

Cheeks, opercles, breast and nape usually scaled. Lateral scale rows 38-64, with 7-44 pored, and 8-46 unpored; transverse scale rows below lateral line 7-10 (usually 8-9), above lateral line 5-7 (6).

First dorsal fin with 8-10 (8-9) spines; second dorsal rays 11-15 (12-14); anal spines 2, anal rays 6-9 (7-8); branched caudal rays 14-17; pectoral rays 10-13 (11-12).

Body proportions: HL/SL 0.26-0.32 ($\bar{X}$ = 0.29); BD/SL 0.15-0.25 (0.21); CPD/SL 0.09-0.16 (0.13); P_1 L/SL 0.16-0.33 (0.23); P_2 L/SL

TABLE 10. Number of transverse scale rows above lateral line in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Scales above lateral line				N	$\bar{X}$	SD
	5	6	7	8			
<i>Etheostoma squamiceps</i>							
Cache River		26	8		34	6.2	0.42
small tribs., Ohio River	8	27			35	5.7	0.42
Wabash River	1	4	8	1	14	6.6	0.71
Tradewater River	2	16	17		35	6.4	0.59
Lower Green River		11	3		14	6.2	0.41
Upper Green River	8	17			25	5.6	0.46
Barren River	3	9	2		14	5.9	0.59
Red River	2	31	8	1	42	6.1	0.54
TOTALS	24	141	46	2	213	6.1	0.59
<i>Etheostoma neopterum</i>							
Clarks River	38	17			55	5.3	0.46
Big Sandy River	11	39	1		51	5.8	0.44
Duck River	6	14			20	5.7	0.45
Shoal Creek	3	22	1		26	5.9	0.39
TOTALS	58	92	2		152	5.7	0.44
<i>Etheostoma crossopterum</i>							
Lower Cumberland River	4	58	4		66	6.0	0.34
Middle Cumberland River	6	40	12		58	6.1	0.54
direct tribs., Mississippi River	2	9	1		12	5.9	0.49
Duck River	9	33	8		50	5.9	0.58
Cypress Creek	16	17			33	5.5	0.50
TOTALS	37	157	25		219	5.9	0.50
<i>Etheostoma nigripinne</i>							
western tribs., Tennessee River	3	33	1		37	5.9	0.32
eastern tribs., Tennessee River	21	9			30	5.3	0.45
southern tribs., Tennessee River	8	40	2		50	5.8	0.43
Shoal Creek	2	24			26	5.9	0.26
Elk River	30	20			50	5.4	0.49
TOTALS	64	126	3		193	5.6	0.42
<i>Etheostoma olivaceum</i>							
Caney Fork River	2	37	55	6	100	6.7	0.62

0.09-0.25 (0.19); PreOL/HL 0.17-0.30 (0.24); EW/HL 0.17-0.32 (0.25); DFH/DFB 0.19-0.59 (0.29).

Coloration of freshly preserved specimens: Coloration similar to *E. squamiceps*. Basic coloration of females and non-breeding males consists of an irregular mottling of brown on light tan background. Dark humeral spot large. Base of caudal fin with three well developed dark spots; middle caudal spot often considerably darker than other two. Dorsum variable, usually colored same as sides, occasionally paler and crossed by 8-9 short, indistinct saddles. Venter usually unmarked. Markings on head typically consist of pre-, post-, and suborbital dark bars. Cheeks often mottled and may have a dark, diagonal line from below eye posterodorsally connecting with postorbital bar at anterior edge of opercle.

First dorsal fin with faint, subdistal orange band formed by row of

TABLE 11. Number of transverse scale rows below lateral line in species of the *Etheostoma squamiceps* species group.

Species & Population	Number of Scales below lateral line							N	$\bar{X}$	SD
	6	7	8	9	10	11	12			
<i>Etheostoma squamiceps</i>										
Cache River		5	18	10	1			34	8.2	0.71
small tribs., Ohio River		1	19	14	1			35	8.4	0.59
Wabash River		2	5	7				14	8.3	0.71
Tradewater River			4	14	13	4		35	9.4	0.84
Lower Green River			4	7	3			14	8.9	0.70
Upper Green River		1	15	9				25	8.3	0.54
Barren River			3	9	2			14	8.9	0.70
Red River		2	12	18	10			42	8.8	0.83
TOTALS		11	80	88	30	4		213	8.7	0.73
<i>Etheostoma neopterum</i>										
Clarks River			16	33	6			55	8.8	0.60
Big Sandy River			11	37	3			51	8.8	0.50
Duck River			12	8				20	8.4	0.49
Shoal Creek	5	20	1					26	6.8	0.57
TOTALS	5	20	40	78	9			152	8.2	0.54
<i>Etheostoma crossopterum</i>										
Lower Cumberland River			17	41	8			66	8.8	0.60
Middle Cumberland River		2	21	33	2			58	8.6	0.61
direct tribs., Mississippi River		1	1	10				12	8.7	0.60
Duck River		9	31	10				50	8.2	0.96
Cypress Creek		6	18	8	1			33	8.1	0.75
TOTALS		18	88	102	11			219	8.4	0.73
<i>Etheostoma nigripinne</i>										
western tribs., Tennessee River		2	26	9				37	8.1	0.51
eastern tribs., Tennessee River		6	21	3				30	7.9	0.53
southern tribs., Tennessee River	1	4	15	27	3			50	8.5	0.80
Shoal Creek		1	16	8	1			26	8.3	0.38
Elk River		14	35	1				50	7.7	0.48
TOTALS	1	27	113	48	4			193	8.1	0.62
<i>Etheostoma olivaceum</i>										
Caney Fork River		2	16	42	32	7	1	100	9.3	0.92

short, vertical bars located between spines. Each bar consists of cluster of dark melanophores overlaid by orange pigment which fades rapidly in preservative. Proximal portion of membrane colorless except for scattered melanophores, sometimes forming indistinct basal band. Base of fin thickened; membrane slightly thickened at tip of spines, forming inconspicuous light colored knobs in both sexes. Soft dorsal fin with clusters of melanophores forming 3-7 interrupted bands plus a rather indistinct basal band; basal part of fin thickened. Caudal fin with melanophores clustered along rays forming 6-8 narrow, dark, vertical bands. Anal and pelvic fins unpigmented; pectorals unpigmented to lightly barred with up to 9 narrow dark bands.

Breeding male coloration: Overall coloration dark (Fig. 8). Sides uniformly dark brown or gray; caudal spots enlarged to form vertical bar; dorsum uniformly dark; venter dark gray; head much darker, almost black, often obscuring regular markings; lower part of head greatly swollen. During courtship and egg-care, sides develop pattern of alternating dark and light bars (Fig. 8). First dorsal fin black except for large light yellow or white knobs on spines and small, clear, round or tear-shaped windows behind each spine; proximal part of fin with narrow clear band; basal part of membrane thickened (Fig. 2). Second dorsal fin black with a broad subdistal white band and 3-6 rows of short, pale dashes across rays, dashes in some specimens appear to connect, forming wavy lines across fin; tips of rays greatly elongated and extending far beyond membrane margin, tips of rays black and lacking the large fleshy knobs of *E. squamiceps* and *E. neopteron* (Fig. 3). Anal fin dark with pale distal margin; membrane thickened around first spine. Pelvic fins dark except for pale membrane around spine and light colored distal band. Caudal and pectoral fins unchanged from non-breeding coloration.

Distribution—*Etheostoma crossopteron* occurs in the lower and middle Cumberland River drainage (except Red River) from mouth east to Plunkett Creek in Smith County, Tennessee and throughout the Duck River system (Tennessee Drainage) in central Tennessee. Isolated populations occur in the headwaters of Caney Fork River in central Tennessee, direct tributaries of Mississippi River in western Tennessee and in Cypress Creek in southern Tennessee and northern Alabama (Fig. 9).

Variation—*Etheostoma crossopteron* shows little sexual dimorphism except for size and pigmentation. Males have more pored lateral-line scales, fewer unpored lateral-line scales, deeper caudal peduncles, smaller eyes ($\alpha = .001$), and a longer preorbital length ($\alpha = .05$) (Table 1). Ontogenetic variation is more pronounced. Small specimens (< 37.5 mm SL) have fewer pored lateral-line scales, more unpored lateral-line scales, larger heads, longer pectoral fins, higher first dorsal fins ($\alpha = .001$), and longer pelvic fins ($\alpha = .01$) (Table 2).

To examine geographical variation, the range of *E. crossopteron* was divided into five areas. The Cumberland River was divided at the mouth of the Red River into an upstream middle Cumberland population and a downstream lower Cumberland population. Additional populations in-

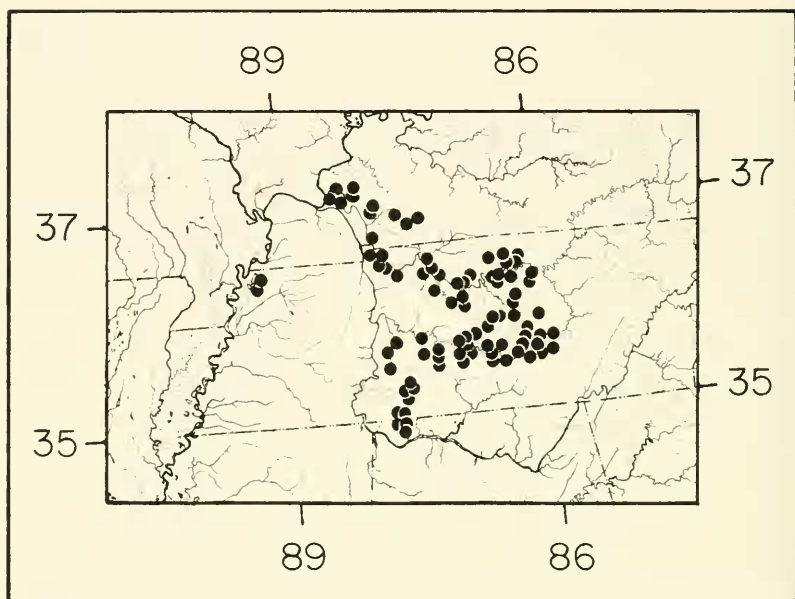


FIGURE 9. Distribution of *Etheostoma crossopterus*.

clude Mississippi River tributaries in the Reelfoot Lake area of Tennessee, the Duck River, and Cypress Creek.

Pigmentation: Although geographic variation in squamation and meristics is extensive, there is little variation in pattern or coloration between populations. Breeding males from the southernmost Cypress Creek population are indistinguishable in body pigmentation or fin shape and pattern from those of the centrally located Duck River or northern Cumberland River. Within any one population, individual variation in degree of breeding coloration attained is far greater than any variation between populations.

Squamation: Several specimens from direct tributaries of the Mississippi River show reduced squamation on the nape, cheeks and opercles (Figs. 5-7). Many specimens from throughout the range, except Cypress Creek, lack scales on the cheek like the related *E. olivaceum* (Fig. 7) which has a naked cheek. Variation also occurs in the degree of scale exposure on the nape and operculum. The highest frequency of exposed scales occurs in specimens from Cypress Creek (Figs. 5, 6).

Meristics and Morphometrics: Anal fin rays, dorsal fin spines, dorsal fin rays, pectoral fin rays, total lateral-line scales, pored lateral-line scales, unpored lateral-line scales, transverse scale rows above lateral line, transverse scale rows below lateral line, HL/SL, P_1 L/SL, P_2 L/SL, CPD/SL, EW/HL, BD/SL, and PreOL/HL all differed significantly between populations ($\alpha = .05$) (Tables 5-12).

Most characters appear to vary in a north-south cline. Although not

included in the tables because of small sample size, specimens from southern tributaries of Buffalo River are intermediate between those of Cypress Creek and the Duck River population. Mississippi River specimens vary independently from the main cline, probably indicating a long isolation from the main gene pool.

Anal rays generally number 7 in all populations except Duck River which averages slightly more (Table 7). Pectoral rays 11 in all populations except Cypress Creek which modally has 12 (Table 8). Scales below lateral line essentially 9 in populations from the Cumberland and Mississippi drainages and 8 in the Duck River and Cypress Creek systems (Table 11). Scales above lateral line modally 6 except Cypress Creek which is bimodal for 5 or 6 (Table 10). Dorsal spines modally 9 except in populations from the Cumberland and Duck systems which have a relatively high proportion of individuals with 8 spines (Table 5). Dorsal rays highly variable between populations, ranging from a mode of 12 in the Cumberland and Mississippi river drainages, to 13 in Duck River and 14 in Cypress Creek (Table 6).

Habitat and Life History—The preferred habitat of *E. crossopterus* is small, quiet streams with large flat rocks or bedrock bottom. In streams of this type in the Nashville Basin, *E. crossopterus* may be the most abundant fish species. Although *E. crossopterus* has the same preferred habitat as *E. squamiceps*, it shows less rigid habitat requirements. Small populations may be found in small gravelly streams and in larger streams along quiet margins and beneath undercut banks. Darter species most commonly associated with *E. crossopterus* are *E. simotermis atripinne* and *E. smithi* in the Cumberland River and *E. luteovinctum* and the golden snubnose darter, *E. (Nanostoma) sp.* in the Duck River. Other species commonly found with *E. crossopterus* are *Campostoma anomalum*, *Pimephales notatus*, *Semotilus atromaculatus*, *Fundulus catenatus*, *Lepomis cyanellus*, and *Cottus caroliniae*.

Page (1974) gives detailed information on reproduction, growth, food habits, population composition, predation, and parasitism on this species from Richland Creek, Cumberland River drainage. As do other species of *Catostomus*, *E. crossopterus* spawns in cavities under rocks and attaches the eggs to the undersides of stones (Fig. 10).

A natural hybrid *E. crossopterus* $\times$ *E. luteovinctum* was collected 21 July 1978 from a tributary of Wartrace Creek, Bedford County, Tennessee by M. E. Braasch, P. W. Mayden, and M. Wright. This is the only known *E. crossopterus* hybrid.

Etheostoma nigripinne NEW SPECIES

Blackfin Darter

Figs. 2, 3, 10, 11.

Holotype—University of Kansas, KU 20000, breeding male 56.5 mm SL (Fig. 11), Pikes Peak Branch, tributary to the Tennessee River 1.6 km W of TN Route 20 bridge, Decatur County, Tennessee, 5 April 1981, Marvin E. Braasch.

Paratypes—A total of 52 specimens deposited as follows: 2—University of Kansas (KU 20894, 50-59 mm SL, same data as holotype); 7—KU 20893 (36-52 mm SL, small tributary to Tennessee River, 0.5 km W Tennessee River on TN Rt. 20, Decatur Co., TN, 14 May 1978); 2—University of Alabama Ichthyological Collection (UAIC 7712.01, 43-49.5 mm SL, same data as KU 20893); 7—University of Michigan Museum of

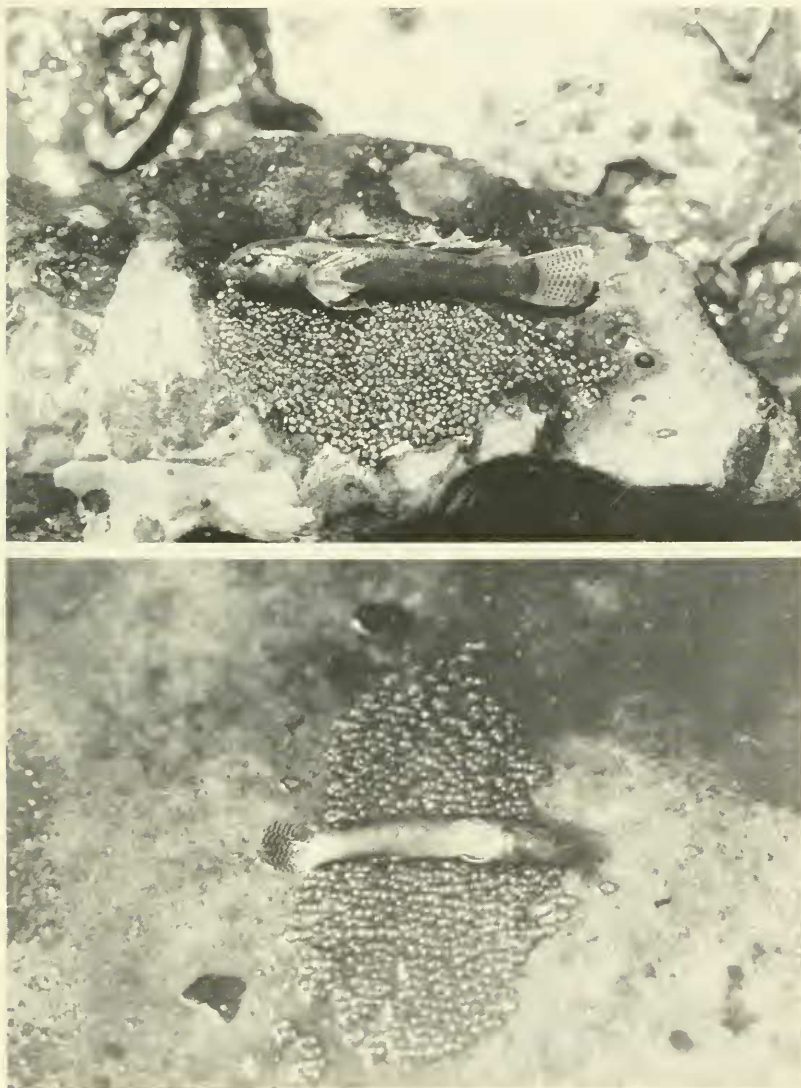


FIGURE 10. Nest-guarding males and eggs of *E. crossopterus* (Top, Bear Creek, Maury Co., TN) and *E. nigripinne* (Bottom, Whites Creek, Decatur Co., TN). Each male was guarding the nest of eggs shown above before their removal. Photographs by Thomas M. Keevin.

Zoology (UMMZ 212481, 28.5-51.7 mm SL, same collection data as KU 20893); 7—United States National Museum (USNM 268083, 35.6-53.3 mm SL, same data as KU 20893); 7—University of Tennessee (UT 91.2768, 35.9-61.5 mm SL, same data as KU 20893); 7—Illinois Natural History Survey (INHS 68092, 33.8-62 mm SL, same data as KU 20893); 7—KU 20895 (36-46.2 mm SL, Whites Creek, 4 mi N Bath Springs, Decatur Co., TN, 4 April 1978); 3—Southern Illinois University at Carbondale (SIUC 9718, 39.8-60 mm SL, same data as KU 20895); 3—Tulane University (TU 139110, 39.3-47.5 mm SL, same data as KU 20895).

Etymology—The specific name, *nigripinne*, comes from the Latin “nigrum” black and “pinna” wing or fin and, along with the common name, refers to the striking black dorsal, anal, and pelvic fins of breeding males.

Diagnosis—Infraorbital canal incomplete; modally 8 transverse scale rows below lateral line, modally 8 dorsal spines and 8 anal rays; cheeks and opercles scaled; breeding males with second dorsal fin lacking pale distal band and without knobs on rays; pelvic and anal fins black; breeding males very dark.

Material examined—Specimens examined during this study, but not designated as types are listed below by drainage and river system.

Western Tributaries Tennessee R.: Decatur Co.: INHS 27485 (19); MEB 109 (37), 152 (3), 153 (15), 154 (1), 155 (7), 156 (1), 157 (12); UT 91.1047 (6), 91.1948 (3), 91.1172 (1).

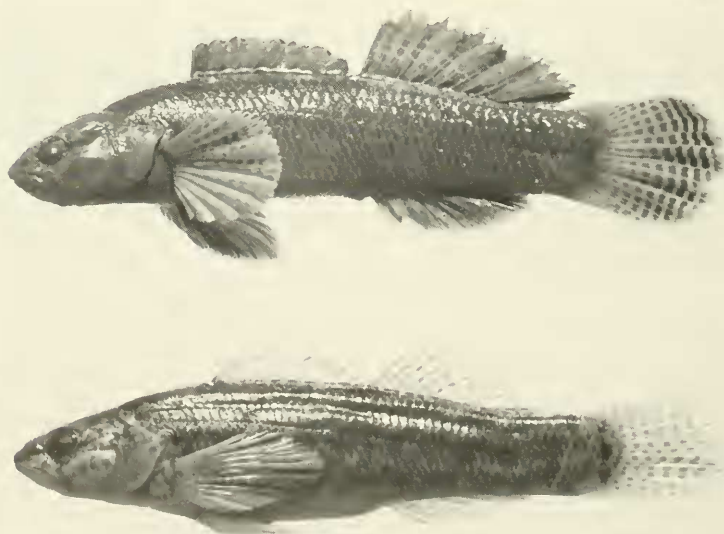


FIGURE 11. *Etheostoma nigripinne*, new species. Top, Holotype, male 56.5 mm SL (KU 20000); Bottom, Paratype, female 43.8 mm SL (KU 20893).

Eastern Tributaries Tennessee R.: Perry Co.: MEB 158 (8), 170 (5); UMMZ 177649 (5). Hardin Co.: MEB 103 (8), 104 (8), 105 (18), 163 (17), 164 (9), 165 (2), 166 (4), 167 (6), 168 (24), 169 (7), 171 (1); UT 91.254 (49), 91.1584 (2), 91.1594 (16). Wayne Co.: MEB 159 (7), 160 (7), 161 (1), 162 (7).

Northern and Southern Tributaries Tennessee R.: Tennessee: Lincoln Co.: MEB 172 (4); UAIC 1972.05 (5), 1974.09 (2). Mississippi: Tishomingo Co.: INHS 76082 (14), 76100 (16); UAIC 1350.04 (1), 2190.11 (5), 2299.12 (1). Alabama: Franklin Co.: KU 20920 (22); MEB 173 (6); UAIC 1883.08 (12), 1914.07 (10), 1921.07 (10), 2131.05 (1), 2132.09 (28), 2133.09 (13), 2135.07 (3), 2177.06 (1), 2178.13 (1), 2325.17 (5), 2522.10 (1); UMMZ 113930 (1). Colbert Co.: UAIC 865.09 (5), 2136.10 (4), 2137.07 (2); UMMZ 114702 (7), 132424 (2), 132485 (1). Lauderdale Co.: INHS 27488 (16); MEB 174 (14); UAIC 2001.11 (1), 2002.01 (22). Lawrence Co.: MEB 175 (4); UAIC 1336.07 (1), 1337.06 (5), 1338.09 (2). Limestone Co.: MEB 176 (1); UMMZ 103760 (1), 114720 (1), 115030 (1), 115064 (1), 159175 (1); UT 91.1423 (143). Madison Co.: UAIC 1966.04 (3), 2543.08 (1). Jackson Co.: INHS 27511 (1); UMMZ 96468 (2). Morgan Co.: MEB 177 (1).

Shoal Creek System: Tennessee: Lawrence Co.: MEB 178 (20), 179 (6); UT 91.98 (5).

Elk R. System: Tennessee: Giles Co.: INHS 75398 (2); MEB 180 (18); UAIC 1978.01 (27), 2704.08 (5), 2794.09 (9), 2796.06 (1), 2869.09 (2), 2871.08 (1), 2872.13 (3), 2873.08 (3), 2955.10 (1), 2956.05 (4), 3201.13 (2), 3202.05 (1). Lincoln Co.: MEB 181 (16), 182 (10); UAIC 1970.04 (15), 1981.04 (3), 2944.03 (3), 2957.03 (3), 2965.16 (1), 2966.13 (21), 2967.12 (3), 2968.14 (21), 2971.06 (2), 2972.09 (12), 3203.17 (2), 3221.02 (3). Franklin Co.: UAIC 1978.01 (1), 2864.15 (8), 2865.14 (1), 2934.02 (2). Marshall Co.: KU 10687 (10), UAIC 2702.04 (1), 2969.03 (3). Coffee Co.: KU 12075 (1), UAIC 2831.07 (1), 2947.05 (14). Moore Co.: UAIC 2940.03 (1), 2948.05 (17). Alabama: Limestone Co.: MEB 183 (14); UAIC 2497.09 (12), 2792.05 (2), 2961.07 (1). Lauderdale Co.: UAIC 1987.05 (4), 3130.13 (2).

Duck R. System: Tennessee: Humphreys Co.: INHS 82932 (7). Bedford Co.: UT 91.2056 (7). Coffee Co.: UT 91.627 (12).

Description—*Etheostoma nigripinne* is one of the smaller members of the *E. squamiceps* group; largest specimen a male 63.5 mm SL. Males generally larger than females, largest female 59.3 mm SL. Specimens of either sex over 55 mm SL are rare. Infraorbital canal incomplete with narrow interruption below eye, pores normally 3-4; preoperculo-mandibular canal pores 10; supraorbital canal pores 4 or 5; supratemporal canal interrupted medially, pores 2-2; lateral canal pores 5; frenum moderate to wide; branchiostegal rays 6, membranes slightly joined or free; preopercle entire to slightly crenulate. Genital papilla of adults enlarged; breeding females with a broad, flat and darkly pigmented papilla.

Cheeks, opercles, breast, and nape usually scaled. Lateral scale rows

42-58, with 10-45 pored, and 6-35 unpored; transverse scale rows below lateral line 6-10 (usually 8), above lateral line 5-7 (5 or 6).

First dorsal fin with 7-10 spines (8); second dorsal rays 11-15 (13-14), anal rays 6-9 (7-8); pectoral rays 10-13 (11-12).

Body proportions: HL/SL 0.27-0.33 ($\bar{X}$ = 0.29); BD/SL 0.15-0.24 (0.21); CPD/SL 0.10-0.16 (0.13); P_1 L/SL 0.20-0.27 (0.23); P_2 L/SL 0.16-0.24 (0.20); PreOL/HL 0.17-0.33 (0.25); EW/HL 0.19-0.32 (0.26); DFH/DFB 0.13-0.44 (0.27).

Coloration of freshly preserved specimens: Coloration similar to *E. squamiceps* and *E. crossopteron*. Basic coloration of females and non-breeding males consists of brown mottling on a tan background (Fig. 11). In larger males, particularly from the southern part of range, mottling tends to coalesce on sides to form a series of 12-13 small dark blotches along lateral line. Small specimens have three dark caudal spots, but most adults retain only the central one. Large dark humeral spot present. Dorsal coloration variable. Specimens from southern populations have 8 dark cross bars; third cross bar larger and darker than others and located between dorsal fins. Cross bars much less prominent in specimens from northern parts of range. Venter normally unmarked. Markings on head typically consist of pre-, post-, and suborbital dark bars.

First dorsal fin with distinct subdistal orange band formed by a row of vertical bars located between spines. Bars consist of clusters of melanophores overlaid by orange pigment. Band much larger and brighter in males than females. Most of membrane proximal to orange band dusted with melanophores—thickly in large specimens, thinly in smaller. Basal portion of membrane thickened; membrane slightly thickened at tips of spines, forming inconspicuous light colored knobs. Soft dorsal fin with clusters of melanophores along rays forming 3-8 interrupted bands plus an indistinct basal band; basal part of membrane thickened. Caudal fin with 6-13 dark vertical bands. Anal and pelvic fins unpigmented; pectorals unpigmented to lightly barred.

Breeding males very dark (Fig. 11); much darker than any other species of the *squamiceps* group. Head, flanks, and dorsum black; venter slightly paler; lower part of head swollen. During egg-care, sides may develop a pattern of alternating vertical light and dark bars, similar to, although more indistinct than, *E. squamiceps*, *E. olivaceum* or *E. crossopteron*. Unlike these species, immediately upon preservation *E. nigripinne* loses these bars and develops the jet black coloration. First dorsal fin black except for large round, pale colored knobs on spines and small round clear windows behind each spine; basal part of membrane thickened and with narrow clear band above basal dark band (Fig. 2). Second dorsal fin in highest males totally black; other males with 1-6 rows of small pale dots or dashes across rays (Fig. 3). Rays elongated past margin of fin in approximately 50% of the specimens. Basal part of fin thickened and sometimes with clear band; distal half of membrane often thickened and partially obscuring black color, giving appearance of gray margin. Anal and pelvic fins black. Caudal fin with dark bands much

enlarged, but usually not touching. Pectoral fins unchanged from non-breeding coloration.

There is variation in breeding color at any one location. Only a small percentage of males will show strong breeding coloration. Whether this is due to a very short breeding period per male or to individual variation is unknown; however great care must be taken when identifying specimens because non-breeding males resemble *E. crossopterus* males in having pale borders to the second dorsal, anal, and pelvic fins.

Distribution—*Etheostoma nigripinne* occurs in tributaries of the Tennessee River from the lower Duck River upstream to the Flint and Paint Rock rivers (Fig. 12). At least two populations are also known from the upper Duck River System in Coffee and Bedford counties, Tennessee, a drainage typically occupied by *E. crossopterus*. Blackfin darters are particularly abundant in the Elk River in southern Tennessee. The status of *E. nigripinne* in Cypress Creek and southern tributaries of the Buffalo River warrants further investigation. Although no specimens are known from either place and both rivers contain populations of the closely related *E. crossopterus*, small populations of *E. nigripinne* could occur in this area. *Etheostoma nigripinne* occurs sympatrically with *E. neopterum* in several creeks in Tennessee and Alabama and possibly with *E. crossopterus* in the Duck River in Tennessee. The occurrence of both *E. nigripinne* and *E. crossopterus* in the Duck system is not unexpected since other researchers have also found close relatives occurring together in this system. Etnier and Jenkins (1980) reported two forms of *Noturus elegans* in the Duck River System and *E. duryi* and "the golden snubnose" both are known from the Duck (Etnier, pers. comm.)

Variation—*Etheostoma nigripinne* shows little sexual dimorphism except for size and pigmentation. Males have deeper caudal peduncles and smaller eyes ($\alpha = .05$) than females (Table 1). Ontogenetic variation is more pronounced. Small specimens (< 40 mm SL) have longer heads, longer pelvic fins, fewer pored lateral-line scales ($\alpha = .05$), larger eyes, and higher first dorsal fins ($\alpha = .001$) than do larger specimens (Table 2).

To evaluate geographic variation, the range of *E. nigripinne* was divided into five areas. Direct tributaries of Tennessee River in Decatur, Benton and Perry counties were designated as western tributaries; Hardin, Indian and Horse creeks in Wayne and Hardin counties, TN were designated as eastern tributaries; all tributaries eastward from Tishomingo County, MS to Paint Rock River in northeast AL with the exception of Shoal Creek and Elk River were designated as southern tributaries; Shoal Creek and Elk River were treated separately.

There is extensive variation in pigmentation, meristics, and proportions between populations of *E. nigripinne*.

Pigmentation: Intensity of pigmentation both in breeding and non-breeding coloration varies clinally from north to south. Individuals from Shoal Creek and Elk River have darker dorsal cross-bars, a darker orange band in the first dorsal fin, and a row of lateral blotches along the lateral

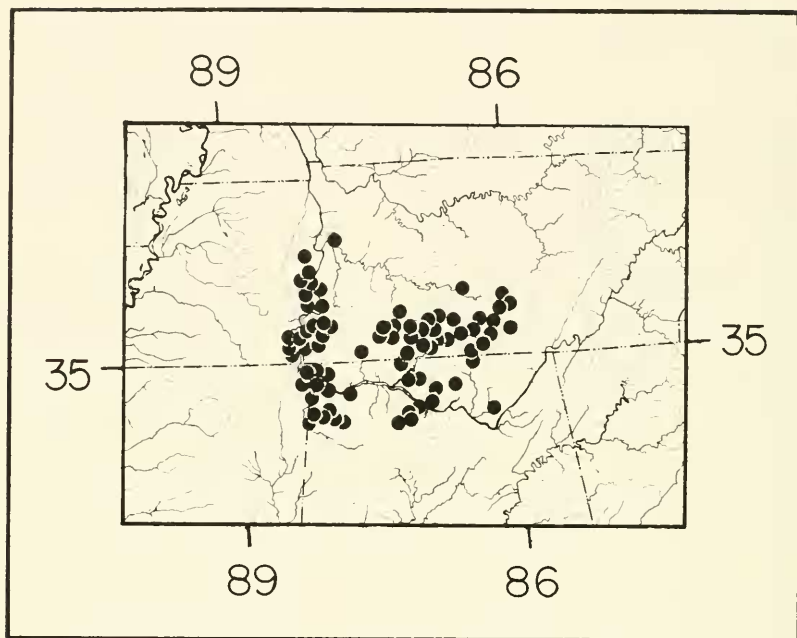


FIGURE 12. Distribution of *Etheostoma nigripinne*.

line. Breeding males from the southern tributaries are usually the darkest, with many individuals being jet black.

Squamation: Little variation occurs with respect to squamation of the head. Most populations have scales on the cheeks, opercles, and nape except in Elk River where a small percentage of the population lacks scales on the cheeks and opercles (Figs. 6, 7). When scales are present they are most commonly embedded although a considerable number of individuals have exposed scales on the nape and operculum (Figs. 5, 6).

Meristics and Morphometrics: Dorsal fin rays, pectoral fin rays, anal fin rays, total lateral scale rows, pored lateral-line scales, unpored lateral-line scales, transverse scale rows above lateral line, transverse scale rows below lateral line, HL/SL, BD/SL, DFH/DFB, CPD/SL, EW/HL, P_1 L/SL, and PreOL/HL all differed significantly ($\alpha=0.05$) between populations of *E. nigripinne* (Tables 6-11, 13).

Most characters varied semi-clinally from upstream to downstream (southeast to northwest). Further, most values were lowest in Elk River and highest in western (i.e., CPD/SL, PreOL/HL, EW/HL) or eastern tributaries (i.e., P_1 L/SL, anal fin rays). A few characters are reversed and have high values at the northern end of the cline (i.e., dorsal fin rays, pectoral rays, pored lateral-line scales).

Habitat and Life History—The preferred habitat of *E. nigripinne* is small bedrock bottom creeks, often less than 1 m wide. A small creek seems to be more important than substrate; in northern Alabama small

TABLE 13. Geographically variable body proportions in *Etheostoma nigripinne*. Measurements and means in hundredths of a millimeter.

Population	N	HL/SL		PreOL/HL		EW/HL		CPD/SL					
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD			
western tribs., Tennessee River	19	27-31	29	0.01	23-31	27	0.03	22-29	25	0.02	13-16	14	0.01
eastern tribs., Tennessee River	26	28-33	30	0.01	18-30	25	0.03	21-29	26	0.02	10-14	12	0.01
southern tribs., Tennessee River	35	26-31	29	0.01	19-33	25	0.04	19-32	27	0.03	9-16	14	0.01
Shoal Creek	10	28-30	29	0.01	23-29	26	0.02	25-32	28	0.02	12-14	13	0.01
Elk River	35	27-32	29	0.01	17-27	23	0.02	22-30	25	0.02	12-15	13	0.01
TOTALS	125	27-33	29	0.01	17-33	25	0.03	19-32	26	0.02	9-16	13	0.01
	N	BD/SL		P ₁ L/SL		DFH/DFB							
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD						
western tribs., Tennessee River	19	20-24	23	0.01	20-25	23	0.01	13-35	24	0.05			
eastern tribs., Tennessee River	26	15-23	20	0.02	23-26	24	0.01	19-33	27	0.03			
southern tribs., Tennessee River	35	18-23	21	0.01	21-26	23	0.01	17-38	28	0.05			
Shoal Creek	10	21-24	22	0.01	21-26	23	0.01	19-44	29	0.07			
Elk River	35	17-23	20	0.02	20-27	23	0.02	20-38	28	0.04			
TOTALS	125	15-24	21	0.01	20-27	23	0.01	13-44	27	0.04			

populations exist in mud bottom creeks where they hide under debris. The darter species most commonly associated with *E. nigripinne* is *E. duryi*, with which it is almost always found. Other species of fishes commonly occurring with the blackfin darter are *Hemitremia flammea* (eastern part of range), *Phoxinus erythrogaster* (western part of range), *Clinostomus funduloides*, *Campostoma anomalum*, *Semotilus atromaculatus* and *Cottus caroliniae*.

Although males begin to acquire breeding coloration in late March and early April, they do not attain full coloration of their dorsal fins until spawning time and begin to lose the coloration after the eggs hatch. Males guarding eggs were found in a tributary of Cane Creek, Lincoln Co., TN on 30 April 1978 and in a tributary of Hardin Creek, Wayne Co., TN on 15 May 1978. Eggs were fastened to the undersides of flat rocks (Fig. 10) as in *E. crossopterygion*, *E. olivaceum*, and *E. squamiceps* (Page, 1974; 1980) and some *E. neopterum* (Page and Mayden, 1979). No other life history data are available.

Etheostoma neopterum HOWELL AND DINGERKUS

Lollypop Darter

Figs. 2, 3, 13.

Etheostoma neopterum. Howell and Dingerkus, 1978.

Types—*Etheostoma neopterum* was described from Little Butler Creek, Wayne Co., Tennessee. Holotype USNM 217529. Paratypes deposited at USNM, CU, AMNH, UMMZ, TU, UAIC, and UT.

Diagnosis—*Etheostoma neopterum* may be separated from all other *Catonotus* in having branches of dorsal fin rays adnate, modally 11-12 dorsal rays, and 12 pectoral fin rays. Rays of second dorsal fin of breeding males elongate and with expanded knobs distally. Second dorsal fin membranes of males with round clear areas.

Material examined—Specimens examined during this study are listed below by drainage and system.

Mississippi R. Dr.: Bayou Du Chien System: Kentucky: Hickman Co.: UL 5992 (1). Graves Co.: KU 20900 (1).

Tennessee R. Dr.: Clarks R. System and Tributaries Lower Tennessee R.: Kentucky: Marshall Co.: INHS 75759 (1), 75784 (3), 77680 (11); KU 12744 (2), 20902 (8); MEB 85 (41); UL 12689 (7), 12867 (18). Calloway Co.: INHS 78268 (1), 75540 (2), 75616 (25), 77602 (2), 77773 (23); KU 20901 (3); MEB 86 (15). Graves Co.: SIUC uncat. (7); UL 12693 (3). Livingston Co.: SIUC uncat. (77).

Big Sandy R. System: Tennessee: Benton Co.: INHS 79348 (2), 79351 (8); KU 16271 (57), 20762 (1); MEB 140 (5), 141 (2), 142 (50); TU 14713 (3); UT 91.194 (37). Henderson Co.: KU 9809 (2). Carroll Co.: KU 9917 (1). Humphreys Co.: INHS 77624 (3), 77810 (23); MEB 143 (3), 144 (6), 145 (9); UT 91.78 (1). Decatur Co.: MEB 91 (2), 146 (8). Henry Co.: INHS 77780 (12). Houston Co.: MEB 147 (3).

Duck R. System: Tennessee: Hickman Co.: INHS 77593 (3), 77786

(2), 77817 (4); KU 14399 (13), 16216 (22); MEB 97 (20). Wayne Co.: MEB 136 (2), 137 (1), 138 (1). Maury Co.: MEB 139 (1). Perry Co.: KU 17684 (8), 20903 (1).

Eastern Tributaries Tennessee R.: Tennessee: Perry Co.: MEB 148 (2), 151 (4). Hardin Co.: MEB 149 (1), 150 (2).

Shoal Creek System: Tennessee: Lawrence Co.: MEB 135 (2), 186 (4). Wayne Co.: CU 64511 (21), 64513 (9). Alabama: Lauderdale Co.: CU 64515 (7).

Description—The following description is based primarily on material at CU, KU, and INHS. Data in parentheses include extreme values reported in Howell and Dingerkus (1978).

Etheostoma neopterum (Fig. 13) is a medium-sized *Catonotus*, with males (up to 63 mm SL) generally larger than females (maximum 61 mm SL). Infraorbital canal complete with 8 pores (northern portion of range) or incomplete, pores 4-3 or 4-4 (southern portion of range); preoperculo-mandibular canal pores 10; supraorbital canal pores 4 or 5; supratemporal canal interrupted, pores 2-2; lateral canal pores 5; frenum moderate; branchiostegal rays 6 per side, membranes free to moderately joined; preopercle entire. Genital papilla enlarged; breeding females with broad and flat papilla.

Cheeks, opercles, breast, and nape usually scaled. Total lateral scale rows 43-55 (usually 41-58), with 14-45 pored and 7-33 unpored; transverse scale rows above lateral line 5-7 (usually 5-6), below lateral line 8-10 (usually 8-9).



FIGURE 13. *Etheostoma neopterum*. Top, male 61.9 mm SL (KU 20900, Bayou de Chien, Graves Co., KY); Bottom, female 55.5 mm SL (KU 9809, Big Sandy River, Henderson Co., TN).

Spinous dorsal with 8-10 spines (usually 8-9); second dorsal rays 10(9)-14 (usually 11-13); anal spines 2, anal rays 6-9 (usually 7-8); pectoral rays 11(10)-13 (usually 12).

Body proportions: HL/SL 0.27-0.36 ($\bar{X}$ = 0.30), BD/SL 0.16-0.22 (0.20); CPD/SL 0.11-0.15 (0.13); P_1 L/SL 0.19-0.27 (0.23); P_2 L/SL 0.17-0.23 (0.20); PreOL/SL 0.19-0.30 (0.24); EW/HL 0.22-0.35 (0.27); DFH/DFB 0.27-0.61 (0.35).

Coloration of freshly preserved specimens: Females and non-breeding males irregularly mottled with brown on tan background, similar to other species of *squamiceps* group (Fig. 13). Large dark humeral spot present, as well as 1-3 dark caudal spots. Head with pre-, post-, and suborbital dark bars. First dorsal fin clear except for orange distal band formed of clusters of pigment; other fins lightly barred to clear.

Breeding males darker, sides grey to dark brown (Fig. 13). First dorsal fin black except for clear basal band, small round clear windows behind spines, and large yellow or white, round, fleshy knobs at tip of each spine (Fig. 2). Second dorsal black except for clear basal band and 2-4 horizontal rows of clear round spots, which may be only anterior to a ray or on both anterior and posterior sides of a ray, occasionally connected by a narrow crescent or semi-horizontal pale line. Tips of greatly elongated rays with large yellow or white fleshy knobs (Fig. 3). Anal and pelvic fins dark, caudal and pectoral fins similar to non-breeding males. More detailed descriptions, including photographs, are given by Howell and Dingerkus (1978).

Distribution—*Etheostoma neopterum* occurs in tributaries of Tennessee River from the mouth south to Shoal Creek in northern Alabama and in tributaries of Mississippi River in western Kentucky (Fig. 14). The lollypop darter is very abundant in the Clarks River area of western Kentucky and the Big Sandy River area of Tennessee and may be the most common species of fish in some small creeks in western Kentucky. In the southern half of its range it is quite sporadic, most collections contain only a few individuals. It occurs sympatrically with *E. nigripinne* in direct tributaries of Tennessee River from Decatur Co., TN south to Shoal Creek, AL and with *E. crossopterum* in Duck River. Because of difficulties in separating small *E. neopterum* from *E. crossopterum* and *E. nigripinne*, *E. neopterum* may be more common in the southern portion of its range than these records indicate.

Variation—Since Howell and Dingerkus did not use specimens from the northern or eastern portions of the range in their description and analysis of variation, data on specimens from the Clarks, Duck, and Big Sandy rivers and Shoal Creek are compared.

Geographic variation is extensive. Anal rays, pectoral rays, dorsal rays, dorsal spines, total lateral-line scales, pored lateral-line scales, unpored lateral-line scales, transverse scale rows above and below lateral line, HL/SL, P_2 L/SL, BD/SL, DFH/DFB, CPD/SL, and EW/HL (Tables 6-11, and 14) varied geographically.

Variation of most characters is commonly in a north-south cline. Duck

TABLE 14. Geographically variable body proportions in *Etheostoma neopterum*. Measurements and means in hundredths of a millimeter.

Population	N	HL/SL			EW/HL			BD/SL		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Clarks River	26	24-31	29	0.01	22-29	26	0.02	16-22	19	0.01
Big Sandy River	21	29-33	31	0.01	23-32	27	0.01	18-22	20	0.01
Duck River	16	29-33	31	0.01	24-33	28	0.02	19-22	20	0.01
Shoal Creek	26	27-31	29	0.01	18-26	21	0.02	20-23	21	0.01
TOTALS	89	24-31	30	0.01	18-33	26	0.02	16-23	20	0.01

	N	P ₂ L/SL			DFH/DFB			CPD/SL		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Clarks River	26	17-21	19	0.01	28-62	34	0.02	11-16	12	0.01
Big Sandy River	21	18-22	20	0.01	27-38	32	0.01	11-14	12	0.01
Duck River	16	19-22	21	0.01	33-45	38	0.02	12-15	13	0.01
Shoal Creek	26	18-23	20	0.01	21-32	29	0.03	10-14	12	0.01
TOTALS	89	17-23	20	0.01	21-62	33	0.02	10-16	12	0.01

River specimens often vary from the Clarks River-Shoal Creek cline. Anal rays usually 7 or 8 in Clarks and Big Sandy rivers, 8 in the Duck River, and 9 in Shoal Creek (Table 7). Pectoral fin rays modally number 12 except in Clarks River where a fairly high percentage of individuals (30%) have 11 (Table 8). Scale rows below lateral line modally 9 in Clarks and Big Sandy rivers, 8 in Duck River, and 7 in Shoal Creek (Table 11). Scale rows above lateral line typically 6, except in a high percentage of Clarks River specimens which have 5 rows (Table 10). Dorsal spines modally 9 except in Duck River where 8 spines are typical (Table 5). Populations from Clarks River modally have 12-13 dorsal rays, those from Big Sandy River and Shoal Creek typically have 11 rays and Duck River specimens have 12 (Table 6).

Other characters which show significant variation include the infraorbital canal and squamation of the head and nape. Specimens from northern populations have the infraorbital canal complete with 8 pores while most specimens from southern populations have the canal incomplete with pores 4-3 or 4-4. Embedded or exposed scales normally present on cheeks, opercles, and nape. Clarks River and Shoal Creek specimens have the highest percentage of exposed scales while Duck River specimens lack exposed scales (Table 3, Figs. 5-7).

Habitat and Life History—Throughout most of its range, *E. neopterum* occurs in small to medium size sandy bottom streams where it hides in and around debris. In Duck River and Shoal Creek it occurs in gravel bottom pools. Like all species of the *squamiceps* group, *E. neopterum* is often found beneath undercut banks and exposed tree roots at margins of pools. Darter species most commonly associated with *E. neopterum* are *E. (Nanostoma) sp.* (red snubnose darter), *E. gracile*, and *E. chlorosomum* in the northern portion of the range, and *E. caeruleum*, *E. simotermum*, *E. spectabile*, *E. flabellare*, and *E. bleunius* in southern and eastern areas.

Other associated species include *Notropis umbratilis*, *Pimephales notatus*, *Semotilus atromaculatus*, *Erimyzon oblongus*, *Fundulus olivaceus*, and *Lepomis cyanellus* in the northern portion of the range, and *Camptostoma anomalum*, *Clinostomus funduloides*, *Notropis boops*, *N. chrysocephalus*, *N. telescopus*, *Semotilus atromaculatus*, *Fundulus catenatus*, and *Cottus caroliniae* in the southern and eastern portions.

Spawning occurs in late April or early May. In suitable habitat, eggs are fastened to the undersides of flat rocks (Page and Mayden, 1979). However, they may fasten eggs to sticks or leaves (Howell and Dingerkus, 1978) as do *E. gracile* and *E. chlorosomum*. A higher percentage of *E. neopterum* males show breeding coloration and dorsal fin morphology than in other species of the group. The reason for this is unknown. Known predators of *E. neopterum* include *Cottus caroliniae* and the salamander *Necturus maculosus* (Howell and Dingerkus, 1978).

Etheostoma olivaceum BRAASCH AND PAGE

Dirty Darter

Figs. 2, 3, 15.

Etheostoma olivaceum. Braasch and Page, 1979

Types—*Etheostoma olivaceum* was described from Rock Springs Branch at Rock Springs Church, 2 km N Buffalo Valley, Putnam Co., TN. Holotype INHS 75734. Paratypes deposited at INHS, USNM, UMMZ, UT, TU, UAIC, NLU, and KU.

Diagnosis—Scales present on nape, prepectoral area, and belly, but absent from cheeks and opercles; transverse scale rows above lateral line usually 7; dorsal fin rays usually 12; infraorbital canal complete; branches of second dorsal fin not adnate; suborbital bar absent.

Material examined—Materials examined during this study include: Tennessee: Dekalb Co.: KU 16214 (7). Putnam Co.: KU 13043 (11). Smith Co.: KU 11442 (33), 14402 (14), 16207 (6). Wilson Co.: KU 11584 (1).

Description—*Etheostoma olivaceum* (Fig. 15) is a moderate sized *Catonotus*; largest specimen a male 67 mm SL, although specimens larger than 55 mm SL are rare. Males generally larger than females, largest female 55.5 mm SL. Infraorbital canal complete with 8 or 9 pores. Total lateral scale rows 44-58, pored lateral-line scales 13-46, unpored 10-37; transverse scale rows above lateral line 5-8 (6-7) and below lateral line 7-12 (8-10); dorsal spines 8-10 (9), with fleshy knobs in both sexes; dorsal rays 11-14 (12-13); anal spines 2, anal rays 6-9 (7-8); pectoral rays 11-13 (12); branched caudal fin rays 14-16.

Coloration of freshly preserved specimens: Coloration of non-breeding males and females variable. Pale individuals have indistinct mottling or vertical bars on a yellow or tan background. Darker individuals may be uniformly dark grey or olive-brown. Head markings consist of pre- and postorbital dark bars. No suborbital bar present. Dark humeral spot present; caudal spots, if present, never darker than other markings. First

dorsal fin with orange subdistal band (fading to brown in alcohol); rest of fin colorless except for scattered melanophores; basal portion of fin thickened; light colored fleshy knobs present on spines. Second dorsal, caudal, and pectoral fins with dark bands; anal and pelvic fins colorless.

Breeding males very dark (Fig. 15). Sides and head uniform brown or black; dorsum and venter somewhat paler. Flesh of head swollen. First dorsal fin black with elongate white knobs on spines and small round clear windows behind each spine; membranes with small black spot distally behind each spine (Fig. 2). Second dorsal fin black with 3-5 narrow gold bands composed of U-shaped markings along each ray. Distal margin of fin pale; rays produced beyond membranes and with black tips (Fig. 3). Caudal fin with broad pale margin and 5-10 narrow gold bands alternating with black bands. Anal fin dark with pale margin. Pelvic fins dark with white knobs on spines. Breeding tubercles absent. For detailed description, variation, and photographs see Braasch and Page (1979).

Distribution—*Etheostoma olivaceum* is restricted to small tributaries of lower Caney Fork River and a few nearby direct tributaries of Cumberland River in central Tennessee (Fig. 14).

Habitat and Life History—*Etheostoma olivaceum* occurs in small bedrock bottom streams where it hides under flat rocks. Occasionally males may be found in quiet riffles. Darter species commonly associated with *E. olivaceum* include *E. simoterum*, *E. flabellare*, *E. caeruleum*, and

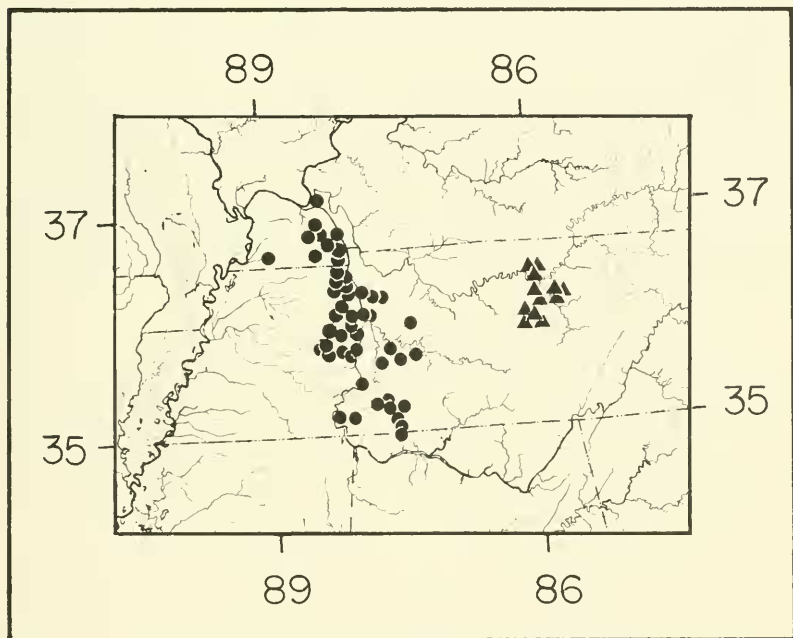


FIGURE 14. Distribution of *Etheostoma olivaceum* (triangles) and *Etheostoma neopterum* (circles).

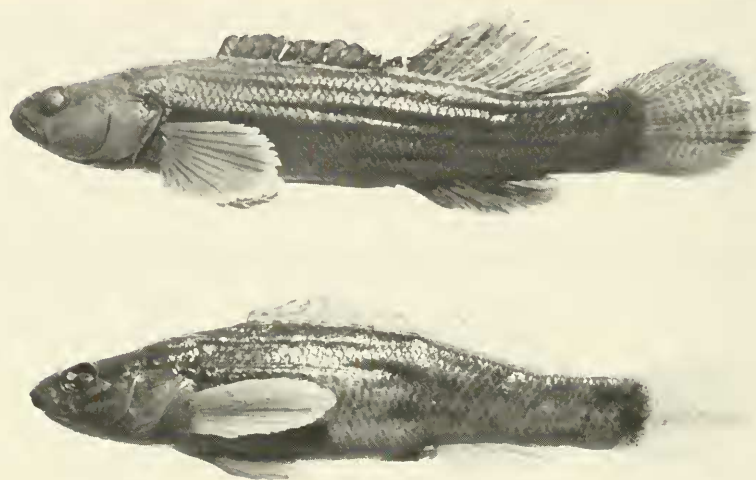


FIGURE 15. *Etheostoma olivaceum*. Top, male 59.3 mm SL; Bottom, female 49.6 mm SL (KU 11442, Dry Creek, Smith Co., TN).

E. spectabile. Other associated species include *Campostoma anomalum*, *Notropis ardens*, *N. boops*, *N. chrysocephalus*, *N. galacturus*, *Semotilus atromaculatus*, *Rhinichthys atratulus*, *Fundulus catenatus*, and *Cottus caroliniae*.

Page (1980) presents a thorough life history of the dirty darter. Maturity occurs at one year for both sexes. Spawning occurs in late March to early May. Mature females produce up to 112 mature oocytes. Eggs are attached to the undersides of flat rocks as in other *Catonotus* and may number as many as 1500. Males are highly territorial and singly attend to nests. Small crustaceans and immature insects comprise most of the diet of young and adults.

SPECIES COMPARISONS IN THE *ETHEOSTOMA SQUAMICEPS* GROUP

Although nuptial males may be easily identified, females and non-breeding males are often difficult to separate. Most species may be separated by range. The only known areas of sympatry are Duck River (*crossopterus*, *neopterus*, *nigripinne*) and direct tributaries of Tennessee River from Shoal Creek north to Decatur and Perry counties, TN (*neopterus*, *nigripinne*).

Counts and Proportions—All adult *E. neopterus* (specimens larger than 40 mm SL) may be identified by adnate branches of dorsal rays. *Etheostoma olivaceum* may be separated from all species except some *E. neopterus* by its complete infraorbital canal (*neopterus* may be complete or incomplete). While no single meristic character is diagnostic, taken as a

group they help to verify identification. *Etheostoma squamiceps* differs from the other species by having shorter pelvic fins, larger eye, lower first dorsal fin, and (along with *neopterum*) fewer unpored lateral-line scales. *Etheostoma nigripinne* differs from others in generally having 8 dorsal spines, 8 anal rays, and 8 lateral scale rows below the lateral line. *Etheostoma crossopterum* can be separated from the other species meristically by having 7 anal rays and 9 dorsal spines. *Etheostoma neopterum* has more anal rays, fewer dorsal rays, and (along with *squamiceps*) fewer unpored lateral-line scales. *Etheostoma olivaceum* has a greater number of unpored lateral-line scales.

Coloration of Breeding Males—Although the basic pattern is similar for all five species, major differences occur in dorsal fin color and morphology. As stated previously, dorsal fin pattern is the last part of the overall breeding coloration acquired and the first lost. The most likely errors would be to confuse sub-breeding *E. nigripinne* or *E. squamiceps* with *E. crossopterum*.

Color of First Dorsal Fin: The basic pattern is to have the membrane black with a small clear spot or window posterior to each spine and a clear basal band. Each spine has a light yellow or white fleshy knob. Males of *E. squamiceps* have small, elongate knobs and the clear windows of the membrane, when present, are narrow vertical slits. *Etheostoma crossopterum* similarly has elongated small knobs, slightly larger than those of *E. squamiceps*, and round or teardrop-shaped windows. *Etheostoma neopterum* has large round knobs on spines and round windows located about $\frac{2}{3}$ of the way up the fin. *Etheostoma nigripinne* has large round knobs and round windows located just below the fleshy knobs. The membranes are much darker in *E. nigripinne* than in the other species and the broad, clear basal band is absent or restricted to only a narrow clear line above a dark basal band. *E. olivaceum* has small elongated knobs, round windows and a clear basal band.

Color and Morphology of Second Dorsal Fin: The basic pattern is a black membrane with several pale cross bars and a clear basal band. Males of *E. squamiceps* have moderately large yellow fleshy knobs distally on branches of each ray; on each ray several U-shaped pale dashes form discontinuous horizontal wavy bands (Fig. 3). Males of *E. crossopterum* lack fleshy knobs and have elongated, black-tipped rays with a sub-marginal pale band; rays crossed by pale semi-horizontal to U-shaped dashes with rows almost touching, forming horizontal pale bands. In *E. neopterum*, large fleshy knobs similar to those of *E. squamiceps* develop on rays but differs in that branches of rays are adnate with one knob per ray (*squamiceps* has two per ray). Fins of northern populations (Bayou du Chien, Clarks, Big Sandy, Duck rivers) of *E. neopterum* have rather large round pale spots anterior to rays, rather than elongated dashes, forming very disconnected horizontal bands (Fig. 3). Lollypop darters from the middle Tennessee tend to develop small clear spots anterior and posterior to rays which may be connected by light concave or horizontal lines. In *E. nigripinne* males with maximum breeding coloration, the fin is totally

black; in males with less than maximum coloration a few horizontal pale dashes are present. Males of *E. olivaceum* have elongate rays with sub-marginal pale band and black tips. Their rays are crossed by several U-shaped light dashes which connect to form wavy horizontal bands.

Coloration of Body: All species for which life history information is available have dark heads and sides with pale horizontal bands. *Etheostoma nigripinne* differs from others in that after preservation the body becomes jet black, while in other species the pale bands remain prominent with the head much darker than the sides.

Coloration of Females and Non-Breeding Males—Coloration of all species is very similar. *Etheostoma olivaceum* differs from all other species except *E. neopterum* from the Duck River in lacking a suborbital bar and by having reduced caudal spots. Most *E. olivaceum* can also be separated by their uniform gray or brown coloration as compared to the irregular mottling of others. Although Howell and Dingerkus (1978) suggested using nape coloration as a character in separating species of this group, it has very limited usefulness because of extreme intra-specific variation.

The presence or absence of an orange or gold stripe in the first dorsal fin is of some diagnostic value. *Etheostoma squamiceps* lacks a band while it is very prominent in *E. nigripinne*. *Etheostoma olivaceum*, *E. neopterum*, and *E. crossopteron* are intermediate. This band is useful for separating sub-breeding male and female *E. nigripinne* from *E. crossopteron*. The bright orange band clearly shows through the dark pigmentation of *E. nigripinne*, while the duller band of *E. crossopteron* is quickly hidden by melanophores.

KEY TO SPECIES OF THE *Etheostoma squamiceps* GROUP

1. Breeding males with distal fleshy knobs on dorsal fin rays (Fig. 3A-B) 2
 Breeding males without fleshy knobs on dorsal fin rays (rays may be elongated) (Fig. 3C-E) 3
2. Dorsal fin rays with 3 branches, anterior branch reaching margin separate from posterior two (Fig. 3A); spinous dorsal fin without orange subdistal band *E. squamiceps*
 Dorsal fin rays with all branches adnate (appearing unbranched) (Fig. 3B); spinous dorsal fin with dull orange subdistal band. *E. neopterum*
3. Infraorbital canal complete with 8 pores, opercle unscaled *E. olivaceum*
 Infraorbital canal incomplete (pores 4-3 or 4-4), opercle scaled. . . 4
4. Second dorsal in breeding males with broad white sub-marginal band, rays elongated with black tips (Fig. 3D); first dorsal with dull orange subdistal band. *E. crossopteron* n. sp.
 Second dorsal fin in breeding males without white submarginal band,

rays elongated or distal part of ray unicolor (Fig. 3E); first dorsal fin with bright, distinct subdistal orange band, not hidden by melanophores *E. nigripinne* n. sp.

ETHEOSTOMA VIRGATUM SPECIES GROUP

The *E. virgatum* species group, or barcheek darters, is a clade of five closely related species. Members occur in the Green, Cumberland, and Tennessee river drainages of Kentucky and Tennessee. Barcheek darters are small to moderately large *Catonotus* characterized by lacking scales on nape, cheeks, opercles, and prepectoral areas; nuptial coloration of males with reds and blues (at least in fins) and by the presence of an iridescent red and white diagonal bar on their cheeks.

Etheostoma virgatum (JORDAN)

Striped Darter

Fig. 16.

Poecilichthys virgatus. Jordan, 1880

Types—*Poecilichthys virgatus* was described from the Rockcastle River at Livingston, Rockcastle County, Kentucky. Lectotype USNM 23456; paralectotype UMMZ 187511.

New Material Examined: Localities in addition to those listed in Page and Braasch (1977) include: Tennessee: Canon Co. creek: KU 20945 (16). Putnam Co., Calfkiller River: KU 11598 (2). Rutherford Co., Overall Creek: KU 20908 (4), MEB (10). Williamson Co., Mayes Creek: KU 20909 (23); MEB (28).

Diagnosis: Fins with reds and blues, face with iridescent red and white diagonal bar; infraorbital canal incomplete, pores 4-2; sides with continuous dark longitudinal lines.

Description—*Etheostoma virgatum* (Fig. 16) is a moderately large *Catonotus* reaching approximately 65 mm SL. Infraorbital canal incomplete, pores 4-2; preoperculomandibular canal pores 10; frenum moderate. Prepectoral area, nape, cheeks, opercles, and breast naked. Total lateral-line scales 38-58, 0-25 pored. Dorsal fin spines 7-10 and with small fleshy knobs; dorsal rays 11-17; anal spines 2, anal rays 7-11; pectoral rays 9-14.

Coloration of freshly preserved specimens: Females and non-breeding males light brown dorsally with six dark brown rectangular saddles. Sides with distinct dark longitudinal stripes formed by a longitudinal, medial row of melanophores through each row of scales. Stripes most distinct on dorsal two-thirds of sides. Sides with a series of nine to 11 rectangular dark blotches. Head dark brown dorsally; well developed preorbital black bar present, suborbital bar weak or absent. Cheek bar with upper portions red or orange, lower portion silvery white and whole bar outlined by gold (fading quickly in preservative). First dorsal fin with black, basal blotch extending from first or second to fifth or sixth spine; remainder of membrane often red. Second dorsal, caudal, and pectoral fins with dark

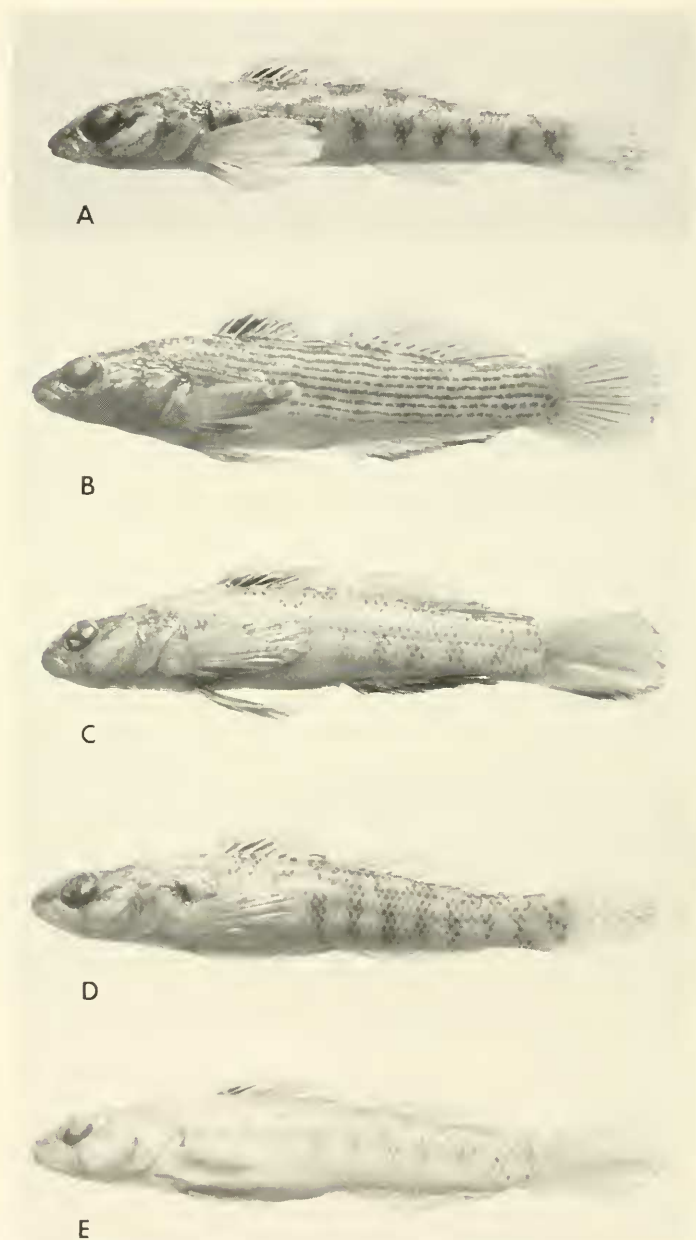


FIGURE 16. Adult males of species of the *Etheostoma virgatum* species group. A) *E. obeyense* (42.1 mm SL, Cumberland Co., KY, 2 April 1966, KU 11552). B) *E. virgatum* (45.7 mm SL, Cannon Co., TN, KU 20945). C) *E. striatulum* (38.5 mm SL, Bedford Co., TN, 5 April 1969, KU 16218). D) *E. smithi* (33 mm SL, Livingston Co., KY, 29 May 1972, KU 16227). E) *E. barbouri* (50.1 mm SL, Adair Co., KY, 8 April 1969, KU 16226).

bands, membranes sometimes with red; anal fin orange, red, or yellow basally.

Breeding males much brighter. Dorsal, caudal, pectoral, and anal fins mostly red; anal, lower caudal, and lower pectoral (and sometimes first and second dorsal) with blue-black margin. Black blotch in first dorsal fin intense; head dark and swollen; cheek bar vivid, lateral stripes dark and distinct.

For a more detailed description, analysis of variation and photographs of adults, see Page and Braasch (1977).

Distribution—*Etheostoma virgatum* may be found in three separate areas in the Cumberland drainage (Fig. 17). These include the Rockcastle River area in KY, upper Caney Fork River in central TN, and tributaries of the middle Cumberland from the Stones to Red River.

Habitat and Life History—*Etheostoma virgatum* occupies a wider range of habitats than do most barcheek darters. They may be quite common in small bedrock creeks, such as those of the Nashville Basin, where they hide beneath flat rocks. They also occupy gravel bottom pools and gentle riffles of larger streams such as in the Rockcastle and Harpeth rivers. As an example of this habitat diversity, in October 1978 two sizeable collections of *E. virgatum* were made in the Harpeth River system, TN. One was from a large stream with moderate current where *E. virgatum* were in large gravel bottom pools approximately 30 m wide and 0.5–1 m deep. The second collection was from a small, almost intermittent bedrock bottom creek approximately 3 m wide and 1.5 m deep. In larger streams, *E. virgatum* is often associated with emergent vegetation, such as *Dianthera*, or it may be found under tree roots or undercut banks; it is also found in slower riffles and gravel bottom pools with no cover.

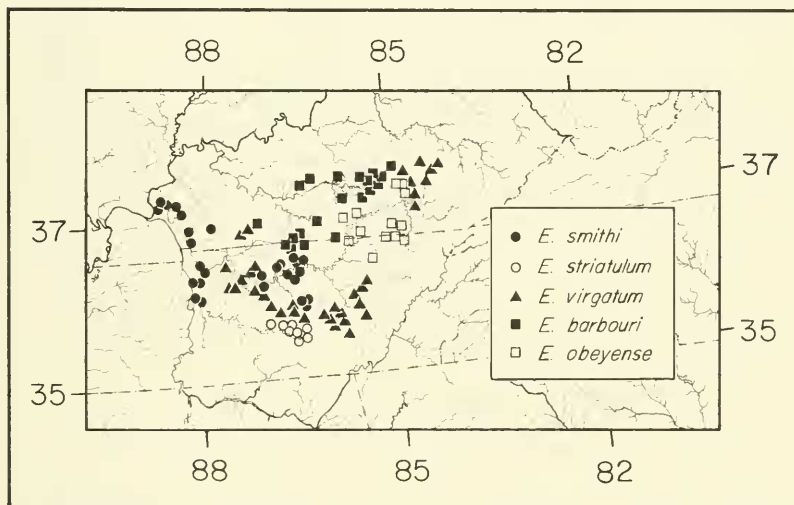


FIGURE 17. Distributions of species of the *Etheostoma virgatum* species group.

Little is known of the biology of this species. Adults are known to fasten their eggs on the undersides of rocks in a manner similar to the other *Catonotus* (Page, 1983). Presumably males guard their eggs until hatching occurs. Kuehne and Barbour (1983) found this species to be one of the first darters to successfully reinvade silted stripmine streams of the Rockcastle System. They also noted several adults in steady current entering small tributaries in April, presumably to spawn.

Etheostoma obeyense KIRSCH

Barcheek Darter

Fig. 16.

Etheostoma obeyense. Kirsch, 1892

Types—*Etheostoma obeyense* was described from several tributaries of Cumberland River, Clinton County, Kentucky. Lectotype USNM 45565, other types in SU, BMNH, and UMMZ.

Material Examined—Localities in addition to Page and Braasch (1976) include: Kentucky: Lincoln Co., Green River: KU 7091 (3).

Diagnosis—Fins with reds and blues, face with an iridescent red and white diagonal bar; infraorbital canal incomplete, pores 4-2; preoperculo-mandibular pores 10; no dark longitudinal stripes on sides; suborbital bar weak or absent.

Description—*Etheostoma obeyense* (Fig. 16) is a large *Catonotus*, reaching 70 mm SL. Infraorbital canal incomplete, pores 4-2; preoperculo-mandibular canal pores usually 10; frenum rather broad; branchiostegal membranes free or slightly connected. Nape, cheeks, opercles, and breast naked; total lateral scale rows 39-56, 10-26 pored; transverse scale rows above and below lateral line 5-9. Dorsal fin spines 8-10 (9) and with fleshy knobs on tips; dorsal rays 12-15 (13); anal spines 2, anal rays 7-10 (9); pectoral rays 11-14 (12).

Coloration: Females and non-breeding males straw-colored dorsally with 6 to 8 dark saddles. Flanks with a series of 9 to 12 vertically elongated dark blotches. Fins identical to those of *E. virgatum*. First dorsal with black basal blotch and some red in membranes; other fins lightly barred and often with some red or orange. Head darker dorsally and with red and white diagonal bar on cheek. Dark preorbital bar present, suborbital bar absent or very weak. Breeding males similar, but with more intense colors, head darker and swollen.

For a more detailed description, analysis of variation, and photographs of adults see Page and Braasch (1976).

Distribution—*Etheostoma obeyense* is found in tributaries of Cumberland River from the Big South Fork west to Obey River in Kentucky and Tennessee (Fig. 17).

Habitat and Life History—The preferred habitat of *E. obeyense* is small bedrock streams where they may be very abundant. In these streams they particularly tend to hide in crevices in the bedrock. Although we have collected *obeyense* from gravel bottom pools in larger streams, they are very rare outside their preferred habitat.

Page et al. (1981) reported on nesting habits of *E. obeyense* from Smith Creek, Clinton Co., Kentucky. Eggs were found attached to the underside of a stone like other *Catonotus*. The 100 eggs were approximately 2 mm in diameter and at various stages of development when found in late May. Nothing is known about spawning habits of this species, although they are presumably similar to those of other barcheeks, where known. Page's (1975a) observations of "*E. obeyense*" spawning habits were later determined to be of *E. smithi* (Page and Braasch, 1976).

Etheostoma smithi PAGE AND BRAASCH

Slabrock Darter

Fig. 16.

Etheostoma smithi. Page and Braasch, 1976

Types—*Etheostoma smithi* was described from Ferguson Creek, Livingston Co., Kentucky. Holotype INHS 75013. Paratypes deposited at INHS, KU, UMMZ, USNM, NLU, TU, UAIC, and UT.

New Material Examined—Localities in addition to those listed in Page and Braasch (1976) include: Tennessee: Trousdale Co., Rocky Creek: KU 20904 (4). Wilson Co., Spring Creek: KU 20905 (5), creek: 20939 (4). Humphreys Co. INHS 77627 (3). Sumner Co., INHS 77497 (7); MEB (18). Caldwell Co., INHS 79368 (3). Rutherford Co., MEB (6).

Diagnosis—Fins with reds and blues, face with an iridescent red and white diagonal bar; infraorbital canal incomplete, pores 3-1; no dark longitudinal stripes or markings on sides; modally 14 dorsal fin rays.

Description—*Etheostoma smithi* (Fig. 16) is a small *Catonotus*, largest specimen 52 mm SL. Infraorbital canal incomplete, pores 3-1; anal rays 8-10 (usually 9), anal spines 2; dorsal spines 8-10 (9); dorsal rays 13-15 (14); pectoral rays 11-13 (12). Prepectoral area, cheeks, opercles, nape, and breast naked; lateral scale rows 41-54, 2-13 pored; transverse scale rows below lateral line 5-9 (6-8), scale rows above 5-9 (6-8). Tips of dorsal fin spines of breeding males with small sub-conical knobs.

Coloration: Coloration in both non-breeding males, females, and breeding males almost identical to those of *E. obeyense*. Differences include a tendency for the lateral blotches to show more vertical elongation in *E. smithi* and the background coloration of *E. smithi* to be darker than *E. obeyense*.

For a more detailed description, analysis of variation, and photographs of adults see Page and Braasch (1976).

Distribution—*Etheostoma smithi* occurs in small tributaries of Cumberland River from the mouth upstream to Wilson and Trousdale counties in central Tennessee and in lower Duck River and nearby Tennessee River (Fig. 17). There are no records for the Red or Harpeth rivers in Tennessee nor the lower Tennessee River in Kentucky.

Habitat and Life History—In the Nashville Basin, the frequented habitat of *E. smithi* is small creeks with a bottom of bedrock. However, in the Duck River they occur in gravel bottom pools and in the lower Cumberland River their habitat is variable, usually pools with either sand,

gravel, or bedrock substrate. They seem to be most common in creeks 5-10 m wide. Occasionally *E. smithi* is found in large rivers. It has recently been collected several times in Cumberland River (Bruce Bauer, pers. comm.). The large river records presumably represent strays and not breeding populations.

Page and Burr (1976) detailed the life history of this species, describing reproduction, growth, food, and population composition in Ferguson Creek, Livingston Co., Kentucky. Males and females attain maturity at one year and live up to 2 years. Young and adults feed primarily on small crustaceans and immature aquatic insects. Spawning occurs between late April and mid-June. Up to 600 eggs are fastened to the undersides of flat rocks where they are guarded by a single male.

Etheostoma striatulum PAGE AND BRAASCH

Striated Darter

Fig. 16.

Etheostoma striatulum. Page and Braasch, 1977

Types—*Etheostoma striatulum* was described from Wartrace Creek, Bedford County, Tennessee. Holotype INHS 75035. Paratypes deposited at INHS, UT, TU, NLU, USNM, KU, UAIC.

New Material Examined—Localities in addition to those listed in Page and Braasch (1977) include: Tennessee: Bedford Co., Hurricane Creek: KU 20950 (4); MEB (1). Marshall Co., INHS 86776 (1); MEB (1), Maury Co., MEB (15).

Diagnosis—Fins with reds and blues, cheek with an iridescent red and white diagonal bar; infraorbital canal incomplete, pores 3-1; dorsal fin spines usually 8; pectoral rays usually 11; sides with dark, longitudinal striations formed by concentrations of melanophores on median and posterior edge of scales.

Description—*Etheostoma striatulum* (Fig. 16) is a small *Catonotus*, reaching 49 mm SL. Infraorbital canal incomplete, pores 3-1; preoperculo-mandibular canal pores 10. Prepectoral area, nape, cheeks, opercles, breast, and nape naked. Total lateral scale rows 38-50, 2-18 pored, transverse scale rows above lateral line 4-6 (5), 6-8 below lateral line. Anal rays 7-10 (usually 9), spines 2; dorsal spines 8-9 (8), dorsal rays 12-14 (13); pectoral rays 10-12 (11). Tips of dorsal spines of breeding males with small round knobs.

Coloration: Color very similar to *E. virgatum*, differing primarily in lateral pattern. Lateral stripes in *E. virgatum* are darker and more continuous than in *E. striatulum*. Stripes in *striatulum* appear discontinuous; because of posterior clusters of melanophores on scales, stripes appear diagonal as well as horizontal. *E. virgatum* usually have 10 or more stripes, whereas *E. striatulum* has 8 or less.

For a complete description, review of variation, and photographs of adults see Page and Braasch (1977).

Distribution—*Etheostoma striatulum* is restricted to small tributaries

of Duck River in Bedford, Marshall and Maury counties, Tennessee (Fig. 17).

Habitat and Life History—The preferred habitat of *E. striatulum* is small bedrock streams characteristic of the Nashville Basin. They tend to congregate near margins of quiet pools where they hide under flat rocks, in vegetation, or beneath under-cut banks or tree roots. At least one collection (University of Tennessee) is known from Duck River proper. Although this probably represents a stray, it indicates that *E. striatulum* is not rigidly restricted to the small creeks.

Page (1980) conducted an intensive life history study on this species. Both sexes reach maturity at one year and live up to 17 months. Adult females produce up to 108 mature oocytes and are significantly smaller than males. Spawning occurs between late March and early May. Eggs are attached to the undersides of flat rocks in the typical *Catonotus* manner and are guarded by a single male. Up to 327 round, translucent eggs have been found in a single nest. As in other barcheeks, the diet of *E. striatulum* varies with age, but consists primarily of small crustaceans and immature aquatic insects.

Etheostoma barbouri KUEHNE AND SMALL

Teardrop Darter

Fig. 16.

Etheostoma barbouri. Kuehne and Small, 1971

Types—*Etheostoma barbouri* was described from Brush Creek, 2.7 mi N Liberty, Casey County, Kentucky. Holotype USNM 204339. Paratypes were deposited at USNM and UMMZ.

New Material Examined—Localities in addition to those cited in Kuehne and Small (1971) include: Kentucky: Adair Co., Petty's Creek: KU 11564 (175), 14406 (22); creek 7080 (6). Lincoln Co., Green River: KU 5809 (7). Tennessee: Sumner Co., Little Trammel Fork: KU 14397 (12).

Diagnosis—Fins with reds and blues, cheek region with red and white iridescent diagonal bar; suborbital bar dark and well developed. Infraorbital canal incomplete, pores 3-1; preoperculomandibular canal pores 9.

Description—The following description is based primarily on specimens at KU and INHS. *Etheostoma barbouri* (Fig. 16) is a small *Catonotus*, maximum size 50 mm SL. Infraorbital canal incomplete, pores 3-1; preoperculomandibular canal pores modally 9. Prepectoral area, cheeks, opercles, nape, and breast unscaled. Total lateral scale rows 40-51, pored 0-16, unpored 29-49; transverse scale rows below lateral line 6-10, scale rows above 2-6 (3-4). Anal spines 2, anal rays 7-11 (9); dorsal spines 7-10 (9), dorsal rays 11-15 (13); pectoral rays 11-13 (12). Tips of dorsal spines of breeding males with small sub-conical knobs.

Coloration: Coloration very similar to *E. virgatum*, differing in the presence of a dark suborbital bar (or teardrop), lateral longitudinal stripes less intense and discontinuous, and lateral blotches larger, more intense, and vertically elongated, sometimes approaching vertical bands. Kuehne

and Small (1971) present a color photograph and a more detailed description and analysis of variation.

Distribution—*Etheostoma barbouri* is restricted to the Green River system where it occurs in Barren River and tributaries of upper and middle Green River (Fig. 17).

Habitat and Life History—The preferred habitat of *E. barbouri* in the Green River system is small to medium size bedrock creeks. In the Barren River system, it is found in gravel or sand bottom pools. Flynn and Hoyt (1979) detailed the life history of *E. barbouri* in Alexander and Little Muddy creeks, Edmonson and Butler counties, Kentucky. Both sexes attain maturity at one year and live up to 2+ years. Males are typically larger than females. Spawning occurs between March and May. Eggs are attached to the undersides of slab rocks and guarded by a single male (Page et al. 1982). In two nests the embryos numbered 42 and 70 and averaged 2.1 mm in diameter. Females produce 17 to 48 mature oocytes depending on age. Oocytes averaged 1.6 mm in diameter. Adults and juveniles feed heaviest during spring and winter months; throughout the year they feed primarily on small crustaceans and immature aquatic insects. Some cannibalism was observed and many teardrop darters were parasitized by *Crassiphiala bulboglossa* and *Contracaecum* sp.

SPECIES COMPARISONS IN THE *ETHEOSTOMA VIRGATUM* GROUP

The *E. virgatum* group consists of two moderate sized (*obeyense* and *virgatum*) and three small species (*smithi*, *striatulum*, *barbouri*). Although differing in color pattern (Fig. 16), there are few differences in meristics between species.

Color Pattern—Three species (*virgatum*, *striatulum*, *barbouri*) have dark longitudinal stripes along sides. These stripes are continuous in *E. virgatum* and broken into dots or striations in *E. striatulum* and *E. barbouri* (Fig. 16). *Etheostoma barbouri* may be separated from *E. striatulum* by the presence of a well developed dark suborbital bar. In addition, *E. striatulum* has posterior markings on each scale giving the appearance of having oblique rows of striations as well as horizontal ones.

Etheostoma obeyense and *E. smithi* lack horizontal stripes and are almost identical to each other in pattern. *Etheostoma smithi* has a darker ground color and more elongated lateral blotches than does *E. obeyense*.

Meristics and Morphometrics—Counts and proportions are very similar in all species. Major differences exist in the number of infraorbital canal pores and pored lateral-line scales. Infraorbital pores are 4-2 in *E. obeyense* and *E. virgatum* and 3-1 in *E. smithi*, *E. striatulum* and *E. barbouri*. *Etheostoma obeyense* and *E. virgatum* also have modally more pored lateral-line scales than the others, although differences between all five barcheeks exist (*obeyense* 17.5, *virgatum* 13.0, *striatulum* 9.6, *smithi* 7.5 and *barbouri* 5.2) (Page, 1981). *Etheostoma barbouri* has modally fewer preoperculo-mandibular canal pores (9 vs. 10 in others); *E.*

striatulum has fewer pectoral fin rays and fewer total lateral-line scales; *E. obeyense* and *E. smithi* have shorter pelvic fins, and *E. obeyense* and *E. barbouri* share a longer preorbital length.

KEY TO SPECIES OF THE *Etheostoma virgatum* GROUP

1. Scales on side with medial row of dark melanophores laterally, forming continuous horizontal stripes (Fig. 16B) *E. virgatum*
 Melanophores not forming continuous horizontal stripes 2
2. Scales on sides, at least posteriorly, with central dark pigment spot formed by group of large melanophores 3
 Scales with melanophores evenly, or randomly, distributed and thus not forming discrete pigment spots 4
3. Preoperculomandibular canal pores modally 10, restricted to Duck River system (Fig. 16C) *E. striatulum*
 Preoperculomandibular canal pores modally 9, restricted to the Green River system of Kentucky and Tennessee (Fig. 16E) . . . *E. barbouri*
4. Infraorbital canal pores 4 (3 + 1), pored lateral line scales 0-10 (Fig. 16D) *E. smithi*
 Infraorbital canal pores 6 (4 + 2), pored lateral line scales 11-30 (Fig. 16A) *E. obeyense*

ETHEOSTOMA FLABELLARE SPECIES GROUP

The *E. flabellare* species group consists of two described and one or more undescribed species. The described species include *E. flabellare* and *E. kennicotti*. The widespread *E. flabellare* is outside the scope of this paper and is only briefly considered here for comparative purposes. This species is presently being studied by Lawrence McGeehan, Ohio State University. Beside the nominal form, two subspecies of *E. flabellare* are currently recognized, *E. f. lineolatum* and *E. f. brevispina*. The earlier recognized subspecies of *E. kennicotti*, *cumberlandicum* was considered invalid by Page and Smith (1976).

Etheostoma flabellare may be separated from *E. kennicotti* by its broadly connected branchiostegal membranes and different color pattern.

Etheostoma kennicotti (PUTNAM)

Stripetail Darter

Fig. 18.

Catonotus kennicotti. Putnam, 1863

Etheostoma cumberlandicum. Jordan and Swain, 1883

Types—*Catonotus kennicotti* was described from a rocky brook, Union County, Illinois. Smith and Page (1975) designated MCZ 24665 as lectotype.

Diagnosis—No red or blue in fins or on body; no red or white diagonal

bar on face; bicolored spinous dorsal, dark distally and clear basally; prepectoral area, cheeks, opercles, and nape unscaled; branchiostegal membrane slightly to moderately connected; anal fin rays usually 7; dorsal rays usually 12.

Material Examined—INHS 972, 983, 1495, 1515, 1575, 1592, 2218, 77899, 88502; KU 14401, 15145, 20911, 20942.

Description—The following description is based on original data and Page and Smith (1976). *Etheostoma kennicotti* (Fig. 18) is a moderately large *Catonotus*. Largest specimens approach 70 mm SL, but most specimens are much smaller. Infraorbital canal incomplete, pores 4-1; cheeks, opercles, nape, prepectoral area, and breast naked. Total lateral scale rows 38-55, with 6-37 pored and 14-40 unpored. Transverse scale rows above lateral line 4-7 (usually 5), below lateral line 6-10 (8). Anal rays 6-9 (7); first dorsal with 6-9 (7) spines, fleshy knobs present in both sexes; dorsal fin rays 10-13 (11-12); pectoral fin rays 11-14 (12-13).

Coloration: Sides yellow to dark brown with 9-11 dark blotches; head darker, particularly dorsally; pre- and postorbital dark stripes present. First dorsal fin colorless except for dark subdistal band and spines sometimes with yellow or orange fleshy knobs (color occasionally extends down onto membrane). Second dorsal, caudal, and pectoral fins with dark bars; anal fin usually colorless. Breeding males with heads darker; flanks flesh-colored to orange with vertically elongated lateral blotches; dorsal spines with conspicuous orange knobs. For a more detailed description



FIGURE 18. Top, *Etheostoma kennicotti*, male 53.8 mm SL (KU 14401, Hatfield Creek, Cambell Co., TN). Bottom, *Etheostoma flabellare*, male 53.3 mm SL (KU 11670, Goose Creek, Trousdale Co., TN).

and analysis of variation see Page (1975a) and Page and Smith (1976).

Distribution—*Etheostoma kennicotti* occurs in the Tennessee, upper Cumberland, Green, and lower Ohio rivers. Although common in the Shawnee Hills and upper Cumberland River, it is sporadic or absent throughout much of the range (Page and Smith, 1976, fig. 2). Wherever it occurs, however, it is often abundant.

Habitat and Life History—Page (1975b), Page and Smith (1976), and Page and Schemske (1978) give the preferred habitat of *E. kennicotti* as slab-rock pools. Throughout most of the range we have found them in gravel or sand-bottom pools or gentle gravel riffles of small spring-fed creeks to mid-sized rivers. Often *E. kennicotti* hides among emergent vegetation at margins of pools or riffles.

Complete life history information of *E. kennicotti* is provided by Page (1975b). Males and females mature in one year and live up to 2+ years. Spawning occurs in April and May when eggs are attached to the undersides of flat rocks. Eggs in nests range from 50 to 400 and are guarded by highly territorial males. Females are generally smaller than males and are known to produce 24 to 130 mature oocytes. Adults and juveniles feed primarily on small crustaceans and immature aquatic insects.

Etheostoma flabellare (RAFINESQUE)

Fantail Darter

Fig. 18.

Etheostoma flabellaris. Rafinesque, 1819

Etheostoma fontinalis. Rafinesque, 1820

Etheostoma linsleyi. Storer, 1851

Catonotus lineolatus. Agassiz, 1854

Oligocephalus humeralis. Girard, 1859

Catonotus fasciatus. Girard, 1859

Richia brevispina. Coker, 1926

Types—*Etheostoma flabellaris* was described from specimens collected in the Ohio River. No types are available as Rafinesque traditionally did not preserve any type material. Based on the drawing illustrated in his notebook, however, there is no problem with the identity of the animal drawn (Collette and Knapp, 1966).

Diagnoses—No red or blue coloration; no scales on cheeks or opercles; branchiostegal membranes broadly connected; transverse scale rows above lateral line usually 7 and below lateral line usually 9.

Description—The following brief description of *E. flabellare* (Fig. 18) is based on Trautman (1957), Cross (1967), and Pflieger (1975) plus specimens from the upper Tennessee and lower Cumberland rivers. This highly variable species probably represents a complex of forms.

Infraorbital canal incomplete, pores 4-2. Nape, cheeks, and opercles unscaled; total lateral scale rows 40-57, 8-37 pored. Transverse scale rows above lateral line 7-9, below lateral line 8-10.

Dorsal spines 7-10, dorsal rays 13-14; anal rays 7-9; pectoral rays 12-13.

Coloration variable. Ground color yellow to black with 10-15 dark crossbars extending to below lateral line. Sides often with longitudinal stripes. Humeral spot dark. Head darker than body, with pre- and postorbital bars. Spinous dorsal with distal and basal orange or brown bands. Spines with fleshy, orange knobs. Soft dorsal, caudal, and pectoral with dark bands; anal and pelvic fins colorless. Breeding males similar, but head darker and with flanks flesh or orange. Orange dorsal fin knobs enlarged.

Distribution—*Etheostoma flabellare* occurs from the east coast west to the eastern Great Plains and south in the Mississippi valley to Mississippi. In the Ohio River system, *E. flabellare* is widespread and common. In the upper Cumberland and the Tennessee River drainages in northeast Alabama and east Tennessee it is common in the Blue Ridge Province along North Carolina border, but is virtually absent in the Ridge and Valley Province (Page, 1983).

Habitat and Life History—*Etheostoma flabellare* occupies quiet to moderate riffles of gravel or rocks. Stream size is of little importance as they can be found in small brooks and large rivers. Considerable work has been done on the growth, reproduction, population dynamics, and diet of this species. This information is summarized by Page (1983). Basically, the biology of *E. flabellare* is similar to other *Catonotus*. Both sexes mature in one year and live up to 4 years. Males live longer than females and are generally larger. Spawning occurs between April and July, but geographic variation has been observed. Eggs are adhesive and are attached to the underside of a flat rock. Spawning occurs beneath the flat rock in cavity excavated by the male. Females produce up to 562 eggs which average 2.2-2.7 mm. As do other darters, *E. flabellare* feeds primarily on small crustaceans and immature aquatic insects.

RELATIONSHIPS

Previous discussions of relationships in *Catonotus* have varied from comments of sister species relationships based on morphology to an electrophoretic examination of six species. Wolfe et al. (1979) examined *E. squamiceps*, *E. flabellare*, *E. kennicotti*, and three barcheek species for three protein systems. They interpreted their results from an unrooted Wagner Network analysis of patristic distances as supporting a close similarity of the *E. virgatum* group, which they equated with this group being natural. Further, they related *E. kennicotti* to *E. squamiceps* and these two species to the *E. virgatum* group rather than either to *E. flabellare*.

Results from morphological studies of the evolution of *Catonotus* are varied. Collette (1966) viewed the subgenus as two major groups, one comprised of *E. squamiceps*, *E. kennicotti*, and *E. flabellare*, all sharing well developed fleshy knobs on dorsal spines. The other group being the *E. virgatum* species group which never or only occasionally develop small

incipient fleshy knobs (Collette, 1966). Page (1975b) evaluated these hypothesized relationships and disagreed with Collette after examining other morphological and breeding characteristics. Page (1975b) considered the *E. virgatum* group to be most closely related to a group including *E. kennicotti* and *E. flabellare* (*flabellare* species group), and he considered *E. squamiceps* to be the most primitive lineage of the subgenus. Kuehne and Small (1971) viewed their new species, *E. barbouri*, as a close relative of *E. virgatum* and *E. obeyense*. Page and Braasch (1976) considered *E. smithi* and *E. obeyense* to be closest relatives, closely related to the other barcheeks, *E. virgatum* and *E. barbouri*. They further noted a close relationship of the clade *E. kennicotti*-*E. flabellare* to all barcheeks. Prior to the description of *E. striatulum*, it had long been considered a close relative of *E. virgatum*, but Page and Braasch (1977) concluded that there is little evidence to consider *E. striatulum* more closely related to *E. virgatum* than to any other barcheek.

Etheostoma squamiceps had long been considered a single species until the descriptions of *E. neopterum* (Howell and Dingerkus, 1978) and *E. olivaceum* (Braasch and Page, 1979). Howell and Dingerkus (1978) placed *E. neopterum* in the *E. squamiceps* group, but considered it more primitive than *E. squamiceps*. Braasch and Page (1979) also considered their new species *E. olivaceum* to be a member of the *E. squamiceps* group and suggested that it was more closely related to the polytypic *E. squamiceps* than to *E. neopterum*.

Our analysis of morphological and behavioral characters presented in the preceding sections of this review and summarized in Appendix 1 and 2 supports a phylogenetic history of *Catonotus* illustrated in Figure 19. We consider the subgenus to be monophyletic with three major subclades—(1) the *squamiceps* species group, (2) the *flabellare* species group, and (3) the *virgatum* species group (Fig. 19). As discussed above, this arrangement of species groups is consistent with previous studies, with the exception of Collette (1966) and Wolfe et al. (1979). Species relationships within the *virgatum* group and *squamiceps* group, however, vary somewhat from previous hypotheses. We believe these inconsistencies stem from grouping species with primitive characters as compared to consistent grouping using derived characters.

Monophyly of Catonotus.—In this analysis the monophyly (i.e. naturalness) of *Catonotus* is supported by 8 characters (Fig. 19). These include (1) an interrupted infraorbital canal, (2) flattened genital papillae in females, (3) spawning occurring on the undersides of stones, (4) presence of fleshy knobs on the tips of dorsal fin spines of males, (5) an incomplete lateral line, (6) a low first dorsal fin, (7) swollen heads in breeding males, and (8) a habitat preference for slab rock pools (See Appendix 1 and 2 for implied transformation series for these and other characters used in this analysis). Character argumentation is presented below.

Most species of *Catonotus* have an interrupted infraorbital canal. Having an incomplete infraorbital canal series is considered derived (Page, 1977; 1981). *Etheostoma olivaceum* and some populations of *E.*

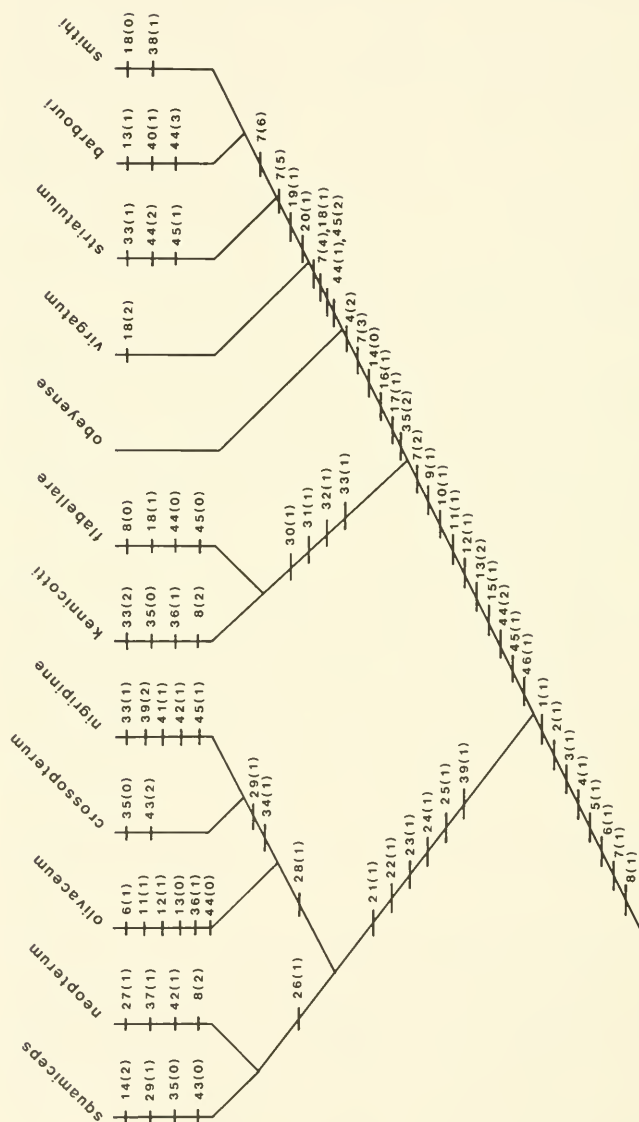


FIGURE 19. Hypothesized phylogenetic relationships of species in the subgenus *Catantotus*. Numbers on branches refer to characters outlined in text and Appendices 1 and 2. Those in parentheses refer to particular states in the hypothesized transformation series of the character.

neopteron have a complete canal, a condition we consider a reversal.

Females of all *Catonotus* have flattened genital papillae, a morphology unique to this subgenus (Page, 1983). Females of *E. sellare* of the subgenus *Etheostoma*, species of the subgenus *Boleosoma*, and species of the *E. maculatum* species group of the subgenus *Nothonotus* also have flattened papillae, but their structures are different and are not considered homologous with the type found in *Catonotus* (Page, 1983).

All species of this subgenus spawn under slab stones (Page et al., 1982). This egg clustering behavior is considered derived and unique to this group of darters. The primitive spawning behavior in darters involves burying eggs in the substrate. Some other darters are known to attach their eggs to the undersides of objects, but certain aspects of their behaviors are quite different from *Catonotus* (i.e. multiple layers of eggs) (Page et al., 1982).

Breeding males of all species of *Catonotus* develop round to elongate fleshy knobs at the tips of their dorsal fin spines (Mayden, 1985). These structures have been reported on several occasions for the *flabellare* and *squamiceps* species groups, but were mentioned only once for the *virgatum* group by Collette (1965). Knobs were reported as missing from the *virgatum* group by Page and Braasch (1976, 1977), Page (1981, 1983), and Page and Burr (1976). Although somewhat smaller than in the other two clades, fleshy knobs are present in the *virgatum* group and are undoubtedly homologous with those of the other species groups, supporting the monophyly of *Catonotus* (Mayden, 1985). Analogous fleshy structures, similar to the knobs of species of *Catonotus*, are also found on spinous dorsal fins of breeding male *Boleosoma*.

All species of *Catonotus* have an incomplete lateral line. We consider the reduced lateral line derived since having a complete lateral line is primitive in darters (Page, 1977). Among the more highly derived barcheeks the lateral line becomes increasingly more reduced.

In *Catonotus* the shape of the first dorsal fin is distinctive. Adults of species of the *squamiceps* and *flabellare* groups have a low first dorsal fin (Figs. 1, 8, 11, 13, 15, 18). Young of these species, however, have higher dorsals relative to the fin base (Table 2), more like adults of other darters. Adult barcheeks, however, have a slightly more elevated first dorsal fin, more like other darters (Fig. 16).

Breeding male *Catonotus* develop greatly swollen heads during courtship, spawning, and egg guarding. We consider this a derived condition in *Etheostoma* since such extreme development is presumably restricted to this subgenus. The development of a swollen head is believed to have a secretory function while guarding eggs (Cross, 1967; Page, 1983).

The habitat preferred by most species of *Catonotus* is distinctive among darters. All species, with the exception of *E. flabellare*, *E. kennicotti*, and *E. neopteron* prefer slabrock pools (Table 15, also see previous discussion of habitat and competition in *Catonotus*, and Page and Schemske, 1978). Although varied, not many other darters can be characterized as preferring this particular type of habitat. We therefore

suggest that this behavioral characteristic is derived for *Catonotus* and has been modified in *E. flabellare*, *E. kennicotti*, and *E. neopterum* (Table 15).

Although the above derived characters of *Catonotus* support the monophyly of the group, the independence of some characters remains to be tested. Five characters 1) flattened papilla, 2) spawning on undersides of stones, 3) fleshy knobs on spines, 4) low first dorsal fin, and 5) swollen heads of males may be correlated and realistically represent a single character complex relating to mode of reproduction. We say this because in other darters and some other fishes when the mode of reproduction involves attaching eggs to the underside of an object some of the above listed characters are sometimes present. Examples include the *Etheostoma maculatum* species group in which some species are known to attach their eggs to the undersides of rocks in fast water and also have a flattened papilla (Page et al., 1982). In the subgenus *Boleosoma* of *Etheostoma* females have flat, bifurcate papillae and males have swollen knobs on dorsal spines. Species of this group are also known to deposit eggs on the undersides of objects (Page, 1983). Further, in the cyprinid genus *Pimephales*, some species attach their eggs to the undersides of debris or stones and males have swollen heads. Thus, the above list of characters may be correlated and represent a single character. However, since in no species outside *Catonotus* can we find complete duplication of all the morphological characters with a similar (but not homologous) reproductive mode (e.g., species of the *E. maculatum* group lack swollen knobs and heads and reduced dorsal fins; *Boleosoma* lack reduced fins and swollen heads) we hesitate to combine all of these characters into one single character complex.

Monophyly of the flabellare-virgatum group.—The sister group relationship of these two clades is supported by 10 shared derived characters (Fig. 19). These include (1) further reduction of the pored lateral line to less than 40%, (2) a naked nape, (3) naked prepectoral area, (4) naked opercles, (5) naked cheeks, (6) a weakly developed suborbital bar, (7) a further reduction of the infraorbital canal, (8) unique nuptial structures on

TABLE 15. Habitat preference of *Catonotus*. 1 = preferred habitat, 2 = less common habitat, 3 = least preferred habitat, x = habitat occupied in restricted portion of range or seasonally.

Species	Sand-Gravel Pool	Slabrock Pool	Gravel Riffle	Slab or Rock Riffle
<i>E. flabellare</i>	x	x	1	1
<i>E. kennicotti</i>	1	2	3	
<i>E. squamiceps</i>		1		x
<i>E. neopterum</i>	1	x		
<i>E. crossopterum</i>	2	1		
<i>E. nigripinne</i>	2	1		
<i>E. olivaceum</i>	2	1		2
<i>E. virgatum</i>	2	1	2	
<i>E. obeyense</i>	2	1		
<i>E. smithi</i>	x	1		
<i>E. barbouri</i>	2	1		
<i>E. striatulum</i>		1		

the ventrolateral body scales of breeding males, (9) a change in scale rows above the lateral line, and (10) a change in the number of scale rows below the lateral line. Changes in the number of scale rows above and below the lateral line are discussed at the end of this section.

All species of the *flabellare* and *virgatum* groups have an increased reduction in the number of pored lateral line scales to 40% or less from the 60-75% pores scales of the *squamiceps* group. As discussed above, having a complete lateral line is primitive for darters. The higher percentage of pored scales in the *squamiceps* group is therefore considered primitive within *Catonotus*.

All species of this group lack scales on the nape, prepectoral areas, opercles and cheeks. These conditions are considered derived in *Catonotus*, since most darters and all other *Catonotus* have scales on these regions. Since *E. olivaceum* can be related to the *squamiceps* group with several characters (Fig. 19) and not with the *flabellare-virgatum* group we believe the loss of cheek and opercle scales in *E. olivaceum* was independent. Further, the occurrence of reduced scales in only two of these four regions in *E. olivaceum* argues for independence of the four regions to scale loss. If these areas were linked in any way such that a loss of scales in one region resulted in a loss of scales in the other regions, then one would expect the nape of *E. olivaceum* to be naked, when in fact it is always scaled. In the *flabellare-virgatum* clade then, the loss of scales in all four regions represents four different independent characters and not a single character—reduced head squamation.

A strongly developed "teardrop" or suborbital bar is common among darters and in the *squamiceps* group. The loss or reduced development of the bar in the *flabellare-virgatum* group is then interpreted here as a shared derived character of this group. *Etheostoma barbouri* is unique among species of this clade in having a well developed bar (Kuehne and Small, 1977).

Species of the *flabellare-virgatum* clade share the loss of the anterior-most pore of the posterior segment of the infraorbital canal. As discussed above, having a complete infraorbital canal is primitive in darters and the interrupted canal of *Catonotus* is derived. Species of the *squamiceps* group usually have four pores anteriorly and 3-4 (usually 3) pores posteriorly. Members of the *flabellare-virgatum* clade have further reduced their head canal system with a maximum of 2 pores in the posterior canal segment. We consider this morphology derived since this is a further step in reduction from a primitive complete system and the *squamiceps* group has a more complete system of 3 pores posteriorly.

The last derived character shared by the *flabellare-virgatum* group is the occurrence of nuptial ridges on the ventrolateral body scales of breeding males. In males with maximum breeding coloration, scales below the lateral line from 6-7 scale rows posterior to the pectoral fin insertion to the caudal fin have centrally located swollen fleshy ridges radiating more-or-less from the center of each scale (Mayden, 1985). Species in the *squamiceps* group and all other darters lack similar structures.

Monophyly of the Etheostoma virgatum group.—The naturalness of the *virgatum* species group is supported by their common possession of at least six derived characters (Fig. 19). These include (1) the presence of an iridescent red and white cheek bar, (2) reduced knobs on the tips of dorsal spines, (3) a further reduction in the number of pored lateral-line scales, (4) a distinctive first dorsal fin pigmentation pattern, (5) a preopercle with a crenulate edge, and (6) 9 anal rays.

All species of the barcheek group have a bright red and white colored bar on both sides of their head covering parts of their cheeks and preopercles. We consider this feature to be derived for this group since it is unique among darters.

Breeding males of all species of *Catonotus* have knobs on the spines of the first dorsal fin (Mayden, 1985). In the *squamiceps* and *flabellare* species groups the knobs are large, but in the *virgatum* group they are small. We believe the most parsimonious interpretation of the distribution of this character is to consider the reduced knob morphology of barcheeks a derived state. Further, if comparisons are made to other taxa with knobs (*Boleosoma*), the knobs present in the *flabellare* and *squamiceps* groups are more like those of these other taxa (in size).

All species of the *virgatum* group share a further reduction of pored lateral-line scales to less than 40% of the total. This is a greater reduction than present in the *squamiceps* and *flabellare* groups. We interpret this further reduction as a derived condition for this group since having a complete lateral line is primitive in darters (Page, 1977).

The dorsal fin pigmentation pattern found in this group is unique among *Catonotus*, as well as other *Etheostoma*. The fin of breeding males is predominantly red with a large intense black basal blotch extending from the first to the sixth spine. Species of the *squamiceps* and *flabellare* groups have an orange band in a darkly pigmented first dorsal fin. We consider the *virgatum* color pattern derived because it is not known to occur in any other darters and the orange band present in the *squamiceps* and *flabellare* groups is commonly shared outside of the subgenus.

The bright coloration of other unpaired, as well as paired, fins in species of this group may also be interpreted as synapomorphic characters. The second dorsal and anal fins of breeding males are predominantly bright red; the caudal fin is red with a blue ventral margin; pectoral fins are reddish medially and blue ventrally; pelvic fins are blue-black. Fins of other *Catonotus* are not brightly colored.

All members of the *virgatum* group share a crenulate preopercle, while other *Catonotus* have a smooth preopercle. Since most darters have a smooth opercle, we consider the crenulate preopercle of the *virgatum* group to be the derived condition. *E. okaloosae* of the subgenus *Belophlox* and some species in the subgenus *Boleichthys* have a serrated preopercle which is quite different from the condition found in the *virgatum* group.

Within *Catonotus* the modal number of anal fin rays varies between species from 7 to 9. The particular distribution of anal fin rays, however, suggests that the ancestral condition in this group was a modal number of 8

rays (Appendix 2). Species of the *virgatum* group uniquely share one of the two derived conditions present in the subgenus, 9 anal rays. The other derived condition, having modally 7 anal rays, has occurred independently in three more primitive members of the subgenus and will be discussed below.

Within the *virgatum* group we consider *E. obeyense* to be the sister taxon to all other presently recognized barcheeks (Fig. 19). This conclusion is based on the observation that other barcheeks share four derived characters, (1) fewer than 35% of the lateral line scales with pores, (2) longitudinal stripes along their flanks, (3) changes in the number of scale rows above, and (4) below the lateral line. We consider these conditions derived since having a complete lateral line is primitive and the longitudinal stripes are nearly unique to this group of *Catonotus*. Longitudinal striations also occur in some parts of the range of *E. flabellare* and have apparently been lost in *E. barbouri*. Changes in the numbers of scale rows above and below the lateral line are discussed below.

Etheostoma virgatum is hypothesized to be the sister group of the three remaining species, *E. striatulum*, *E. barbouri* and *E. smithi* (Fig. 19). The latter three species share three derived characters not shared with *E. virgatum*, (1) reduction of the anterior segment of the infraorbital canal to 3 pores, (2) reduction of the posterior infraorbital canal to one pore, and (3) reduction to approximately 25% or less of the lateral body scales with pores. The reduction in the number of infraorbital pores is considered derived since having a complete infraorbital canal is primitive in darters and having 4 anterior and 2 posterior pores is primitively shared with other *Catonotus* as well as other *Etheostoma*. The pored lateral line reduction is considered derived because it represents a further modification from the primitive complete condition. The presence of only three pores in the anterior infraorbital canal segment is unique to this group of *Catonotus*, but the reduction to one pore in the posterior segment is also known to occur in *E. kennicotti* (Fig. 19).

Among the remaining three barcheek species, *E. barbouri* and *E. smithi* are hypothesized to be sister species, most closely related to *E. striatulum*. *Etheostoma barbouri* and *E. smithi* share a more derived condition of the lateral line in having a reduction to fewer than 20% of the scales being pored.

Monophyly of the E. flabellare group.—At least four shared derived characters corroborate the monophyly of this species group (Fig. 19). These include (1) a modal number of 7-8 dorsal fin spines, (2) very large knobs on dorsal spines, (3) knobs on dorsal spines being golden, and (4) the presence of these knobs on both males and females.

The modal number of dorsal spines varies in *Catonotus* from 7 to 9. The distribution of the modal number of spines indicates that primitively *Catonotus* had 9 dorsal spines (Appendix 2). Changes from this condition to 8 and 7 have occurred three times, once to 8 and 7 in the *flabellare* group and twice to 8 in *E. nigripinne* and *E. striatulum* (Appendix 2). We

therefore consider the reduction to 8 and 7 dorsal spines in *E. flabellare* and *E. kennicotti* to represent evidence of their monophyletic origin. Since *E. flabellare* is a wide-ranging species with variation in the number of dorsal spines this species may actually represent a polytypic member of the subgenus with some geographic forms (those with a mode of 7 dorsal spines) more closely related to *E. kennicotti* (which modally has the further derived state of 7 spines) than to other *E. flabellare* with modally 8 spines.

Further corroborating the monophyly of this species pair are the well-developed knobs on dorsal spines, their presence in both males and females, and their bright golden color. In members of the *squamiceps* and *virgatum* groups knobs are opaque to light yellow. In both of these groups females do not develop these structures and the size of knobs in breeding males is reduced compared to males of *E. flabellare* or *E. kennicotti*. Thus, because of the shared nature of these characters between the non-sister groups (*squamiceps* and *virgatum* groups) we interpret the conditions shared in the *flabellare* group derived.

Monophyly of the Etheostoma squamiceps group.—The monophyly of this species group is supported by their sharing at least six advanced characteristics (Fig. 19). These include (1) three distinct dark spots at the base of the caudal fin, (2) rays of the second dorsal fin of breeding males extending well beyond the fin margin, (3) having clear windows in the heavily pigmented membranes of the first dorsal fins, (4) having a wide subdistal white band in the second dorsal fin, (5) spawning adults only briefly inverting to spawning surface, and (6) females spawning more than one egg at a time.

Having rays of the second dorsal fin extending beyond the fin margin is apparently unique to this species group of darters. In other *Catnotus*, as well as other darters, the fin edge may be rough with high points corresponding to tips of fin rays and lower areas in between represented by a slightly lower membrane, but never do the rays extend out beyond the membrane as in members of the *squamiceps* species group (Fig. 3).

The first dorsal fin pigment pattern found in males of this group (Fig. 2) is, again, presumably unique. Other *Catnotus* species lack any development of clear windows in the fin membranes and we are unaware of any similar development of this pattern in other darters.

Breeding behavior may also serve to support the monophyly of this species group. Page (1975b) compared the spawning behaviors of the different species groups of *Catnotus*. He examined variation in the inversion behavior of males and females to the spawning surface and the number of eggs spawned at one time. Where known, males of the *flabellare-virgatum* group lay 1 egg at a time on the breeding surface and remain inverted for several hours (Page 1975a, b; 1983). Spawning behaviors are known for 3 of the 5 species of the *squamiceps* group, *E. squamiceps*, *E. crossopterum* (Page, 1974, 1975b) and *E. olivaceum* (Page, 1980). No data are available for *E. neopterum* and *E. nigripinne*, although we would predict, as did Page and Mayden (1979), their

behaviors to be very similar. In the *squamiceps* group the male and female only briefly invert to deposit more than one egg at a time (Page, 1974). Therefore, there are presently two modes of spawning in *Catonotus*, representing two characters, duration of female inversion and the number of eggs spawned with each inversion. Either a female is inverted for an extended period of time and spawns a single egg at a time, or they invert only briefly and spawn up to three eggs at a time.

Since depositing eggs on the undersides of stones is a rare behavior in darters, it is difficult to determine the polarity of these behaviors. However, if comparisons are made with other *Etheostoma* with this type of reproduction then behaviors found in the *flabellare-virgatum* group can be considered primitive. Species with similar reproductive activities include the subgenus *Boleosoma* (Page et al., 1981) and some members of the subgenus *Nothonotus* (Page et al., 1982). At present spawning behavior is known only for species of *Boleosoma*, and in this group females remain inverted beneath the spawning surface for several hours and deposit eggs one at a time (for summary see Page, 1983), like the *flabellare-virgatum* group.

Within the *squamiceps* clade *E. squamiceps* and *E. neopteron* are considered sister species (Fig. 19). These two species together form the sister group to the remaining species *E. olivaceum*, *E. crossopteron*, and *E. nigripinne* (Fig. 19). The sister group relationship between *E. squamiceps* and *E. neopteron* is evidenced by their sharing the unique morphology of having the tips of their second dorsal fin rays being expanded into knobs (Figs. 1, 3, 13) and not pointed or flat as in other *Catonotus* (Fig. 3) as well as other darters. We consider this morphology derived since it is unique among darters.

The monophyly of *E. olivaceum*, *E. crossopteron*, and *E. nigripinne* is supported by their sharing an advanced color pattern of the second dorsal fin. Breeding males of all three species have black tips on rays of the second dorsal fin. We consider this color pattern derived since second dorsal fin ray tips of other *Catonotus*, including *E. squamiceps* and *E. neopteron*, are pale during all seasons of the year. Males of *E. nigripinne* differ from the other two species in that the black tips of rays, dorsal to a broad white subdistal band, are obscured in maximally colored spawning males by a complete blackening of the fin (Figs. 3, 11). However, males of *E. nigripinne* prior to spawning have the black tips and a white subdistal band like *E. crossopteron* and *E. olivaceum*.

Within this group of three species relationships are close, but we consider *E. nigripinne* and *E. crossopteron* to be more closely related to each other than either is to *E. olivaceum* (Fig. 19). This relationship is supported by their sharing modally 11 pectoral rays and white horizontal to semi-horizontal dashes in the second dorsal fin. The primitive modal number of pectoral rays in the subgenus *Catonotus* and in the *squamiceps* species group is 12. Changes from this condition have occurred three times in the evolution of *Catonotus*, once in *E. striatulum* and twice in the *squamiceps* group (once in *E. squamiceps* and once in the common

ancestor of *E. nigripinne* and *E. crossopterus*). *Etheostoma olivaceum* and *E. neopterus* have retained the primitive condition of having modally 12 pectoral fin rays. One may wish to view the distribution of this character in the *squamiceps* group as an early change from 12 to 11 in the ancestor of the *squamiceps* group and later independent reversals to the primitive condition in *E. neopterus* and *E. olivaceum*. This is congruent with our hypothesized phylogeny, but is not the most parsimonious explanation. It requires additional steps to explain the evolution of this character. An equally parsimonious scenario as the one we have chosen to adopt here would be the evolution of 11 rays in a common ancestor of the *squamiceps* group and a reversal to 12 rays in a common ancestor of *E. neopterus* and *E. olivaceum*. This hypothesis, however, is in conflict with other characters and is not adopted here.

When present, depigmented dashes in the second dorsal fin in *Catonotus* vary from being U-shaped to horizontal dashes. *Etheostoma squamiceps*, *E. olivaceum*, *E. flabellare*, and *E. kennicotti* all have several U-shaped pale dashes crossing rays of the second dorsal fin (Figs. 1, 3, 15, 18). In *E. neopterus* the pale areas are generally large dots (Figs. 3, 13) and in the barcheeks pale areas are absent. In breeding males of *E. nigripinne* and most males of *E. crossopterus* the pale areas are in the shape of horizontal dashes. This character appears to be fixed in *E. nigripinne*, but is more variable in *E. crossopterus* as males with a semi-horizontal pattern exist. Aside from having the fixed horizontal pattern, *E. nigripinne* differs from *E. crossopterus* (and other species) in having only a few rows of very small horizontal pale lines in the second dorsal fin and having a completely black fin in males with maximum breeding coloration.

Additional characters.—Because of the inherent variability of some meristic data between outgroups and within species it is difficult to determine some polarities *a priori* in *Catonotus*. However, once less variable characters are logically polarized, data from these meristic characters may then be examined for their probable evolution in *Catonotus*, trying in each case to minimize the number of steps necessary to explain the evolution of the characters in the subgenus. Characters included here are numbers of dorsal rays, dorsal spines, anal rays, and transverse scales above and below the lateral line (Fig. 19, Appendix 1 and 2).

Interpretation of the number of anal fin rays was briefly discussed above under the monophyly of the *virgatum* and *flabellare* groups. Eight anal rays appear to be the condition most likely present in the common ancestor of *Catonotus*. This condition is present in *E. kennicotti* and all species of the *squamiceps* species group except *E. squamiceps* and *E. crossopterus*. The occurrence of seven rays in these latter two species is considered convergent because of conflict with other more conservative characteristics suggestive of alternate relationships (Fig. 19). As discussed above, the occurrence of 9 anal rays in all species of the *virgatum* group is interpreted as an independent development from the ancestral mode of 8.

The evolution of dorsal spines is discussed briefly under the mono-

phyly of the *flabellare* group. All *Catonotus* have 9 dorsal spines except *E. nigripinne*, *E. striatulum*, and most *E. flabellare*, which typically have 8 and *E. kennicotti* which modally has 7. With reference to relationships in *Catonotus* (Fig. 19) we therefore consider a mode of 9 dorsal spines to be primitive in *Catonotus* and 8 spines to be derived independently in *E. nigripinne*, *E. striatulum*, and the ancestor of the *flabellare* group. In the *flabellare* group further reduction has occurred in some *E. flabellare* and *E. kennicotti*, with 7 spines.

Interpretation of the evolution of dorsal fin rays is somewhat less confusing. Modal numbers of dorsal rays in *Catonotus* varies from 11 to 14. The most parsimonious explanation of the evolution of this character would be that primitively in this subgenus the modal number of dorsal rays was 13, since primitive members of all clades have this number. Changes have occurred twice in the *squamiceps* group, once in *E. neopteron* with 11 rays and once in *E. olivaceum* with 12 rays. Among the remaining *Catonotus*, *E. kennicotti* shifted to a mode of 12 and *E. smithi* typically has 14 rays.

Transverse scale rows above and below the lateral line are more difficult to interpret. With reference to the phylogeny (Fig. 19), however, one may hypothesize that the ancestral *Catonotus* species had 6 scale rows above the lateral line. A change occurred only once in the *squamiceps* group, in *E. olivaceum* which modally has 7 scale rows. A change from 6 to 5 scale rows in the ancestral species of the *flabellare-virgatum* group is congruent with the phylogeny presented above. This was modified with a change to 7 rows in *E. flabellare* and a reversal to 6 rows in the ancestral species of the *virgatum-striatulum-barbouri-smithi* clade. Within this latter group, changes to 5 and 4 scale rows occurred in *striatulum* and *barbouri*, respectively. This interpretation of the evolution of the modal number of scale rows above the lateral line is one of many, but is most congruent with the evolution of other characters.

The evolution of scale rows below the lateral line in *Catonotus* is equally perplexing. The modal number of rows varies between 7 and 9. Nine rows appears to represent the primitive condition in *Catonotus* and is present in all the *squamiceps* group species (except *E. nigripinne*) and *E. flabellare*. *Etheostoma kennicotti* and *E. obeyense* either independently evolved 8 scale rows from the primitive 9 or the ancestor of the *flabellare-virgatum* group evolved 8 and *E. flabellare* reversed back to modally having 9. The ancestral species to the *virgatum-striatulum-barbouri-smithi* group evolved 7 scale rows from the ancestor of the *virgatum* group, which presumably had 8 rows. *Etheostoma striatulum* is at variance with its closest relatives in having reversed its number of scale rows below the lateral line to 8.

These are but just a few of the many possible evolutionary interpretations of meristic variation in *Catonotus*. We have chosen to prefer the above scenario over alternative scenarios because of minimal conflict with other more stable characteristics.

ZOOGEOGRAPHY

Although all 12 described species of *Catonotus* occur in the same general area, regions now drained by the Cumberland, Tennessee, and lower Ohio river drainages, we know of no case in which more than four species can be found at a particular locale. As discussed briefly under each species group and by many biogeographers, the distribution of a species is controlled by geological or ecological barriers and dispersal routes. Within the range of a species, its presence or absence in a particular stream is dependent on the availability of suitable habitat, and given that suitable habitat exists, competition between species may make suitable habitat unavailable. Below we discuss the biogeography of the subgenus *Catonotus* with respect to possible origins of the various species and attempt to correlate distributional patterns with available geological and drainage histories of the region. In addition, the maintenance of these species distributions are discussed with reference to habitat availability and interspecific competition.

The complex distributional patterns of species in *Catonotus* together with the embryonic state of our knowledge of the subgeneric relationships of darters and our limited understanding of the early geological history of the region makes it difficult to determine the antiquity of this group and its geographic origin. The large degree of sympatry between and within groups and the high diversity of *Catonotus* in the Cumberland River drainage implies that the subgenus may be quite old (probably mid-Tertiary) and had its origin in the Cumberland drainage.

Etheostoma squamiceps group.—The earliest division of this group was the separation of the *squamiceps-neopteron* ancestral species from the ancestor of *E. crossopteron*, *E. olivaceum* and *E. nigripinne* (Fig. 19). Presumably, the ancestor of the *squamiceps-neopteron* pair gained access to the Ohio River from the Cumberland drainage and both differentiated from their ancestral form. The exact means by which these two species pairs became isolated is problematical. One scenario is that access to the Ohio drainage was gained at some date when the Ohio and Cumberland rivers formed a single system and the event(s) correlated with the initial speciation event was the separation of these two river drainages (Fig. 20A). Thus, there would have been a widespread "*squamiceps*" ancestral species in the Ohio and Cumberland river drainages which gained access to both of these drainages prior to our existing preglacial drainage patterns, over a landscape unknown to us today. The vicariance event leading to the separation of the two ancestral species, one in the Ohio and one in the Cumberland, involved drainage alterations which culminated in our existing pre-Pleistocene patterns of the Ohio and Cumberland rivers where both flowed independently into the Coastal Plain (Fig. 20A).

An alternative scenario is that the ancestral "*squamiceps*" species gained access to the Ohio River drainage through stream capture between the two drainages. The most likely area involved would be capture between a tributary of the Cumberland River by a tributary of the Barren

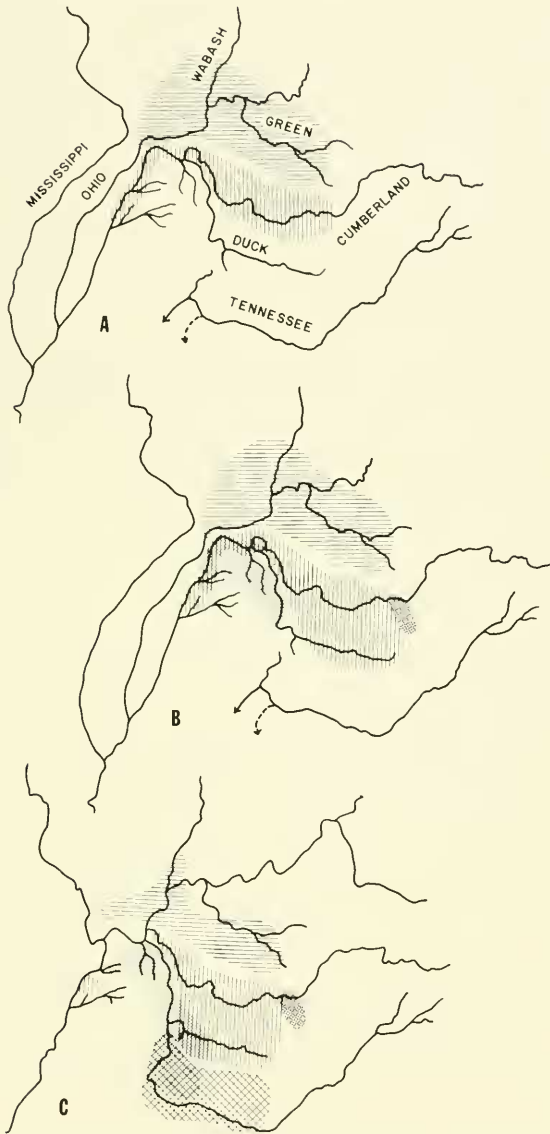


FIGURE 20. Hypothesized biogeographic history of the *squamiceps* species group. (A) Preglacial drainage patterns and distributions of ancestral species of the *squamiceps-neopteron* pair (horizontal) and *olivaceum-crossopteron-nigripinne* group (vertical). Drainage patterns from Thornbury (1965), Pflieger (1970), and Starnes and Etnier (in press). (B) Late Tertiary-early Pleistocene drainage patterns with *E. squamiceps* in the Ohio drainage, *E. neopteron* (stippled) in the lower Cumberland-Duck drainage, *E. olivaceum* on eastern Highland Rim and ancestor of *E. crossopteron* and *E. nigripinne* in the Cumberland and upper Duck drainages. (C) Late Pleistocene capture of middle and upper Tennessee system by Duck system and movement of *E. neopteron* and *E. nigripinne* (form) into Tennessee drainage, with differentiation of the latter.

River. Tributaries of these two rivers interdigitate in northern Tennessee and the divide is easily breached. Having gained entry into the Green River, it could have easily spread throughout the upper Ohio drainage (which was small at the time) (Fig. 20A) and attained a range now occupied by *E. squamiceps* (Fig. 20A).

Separation of the Ohio River form into *E. squamiceps* and *E. neopterum* probably occurred when a population became isolated in the lower Cumberland River drainage, which at that time basically paralleled the Ohio River (Fig. 20A). The most likely area of connection is a break in the divide near Karnak, Pulaski County, Illinois, which today is occupied by a drainage canal. Once in the lower Cumberland drainage it diverged from *E. squamiceps* and became distributed in sandy bottom tributaries of the upper Mississippi Embayment from the Obion River in western Kentucky to the mouth of the Duck River. It would have been absent in the middle Tennessee since at this time the middle and upper Tennessee River were not connected to the present lower Tennessee, but had a separate entry into the Coastal Plain and the Gulf of Mexico through eastern Tennessee or northern Mississippi (Starnes and Etnier, in press) until mid-to late Tertiary (Fig. 20B). Thus, no *Catnotus* was in this portion of the present-day Tennessee River system. This is further supported by the absence of any representative of the subgenus in gulf drainages. Movement of *E. neopterum* into the middle Tennessee could not have occurred until late Tertiary when a temporary drainage advantage in the middle and upper Tennessee captured the Duck River (Starnes and Etnier, in press).

The Cumberland River form attained a distribution in the Preglacial Cumberland drainage as far downstream as what is now northwest Tennessee (Fig. 20A and B). In the Mississippi Embayment this form was probably restricted to small streams along bluffs immediately adjacent to the river and was probably never common or widespread. The absence of appropriate habitat in the lower portions of the Duck River where it passed through the lowland Mississippi Embayment precluded its entry into the system. Access to the Duck system did not occur until the Pleistocene when the center of Highland Rim peneplain, formed in the Miocene (Thornbury, 1965), hollowed out to form the Nashville Basin. Development of this low relief basin may have allowed the Cumberland form to gain access to the Duck through stream capture. Correlated with the development of the Nashville Basin was the isolation of a population in the Caney Fork system on the eastern remnant of the Highland peneplain (Fig. 20B). This eastern population differentiated into *E. olivaceum*.

Later in the Pleistocene, the middle and upper portions of the present-day Tennessee River were captured by the Cumberland drainage (Fig. 20C), thus creating drainage patterns of today (Starnes and Etnier, in press). This event was instrumental in allowing the Nashville Basin and lower Cumberland form (ancestor of *crossopterum* and *nigripinne*) to gain access to the middle Tennessee River drainage and later differentiate into *E. nigripinne* (Fig. 20C). Factors responsible for separating these two forms and promoting their differentiation would most likely have been the

marginal habitat of the western Highland Rim. Alternatively, one may hypothesize that the ancestor of *E. nigripinne* may have been introduced into tributaries of the middle Tennessee River through stream capture across the Duck-Tennessee divide, thus isolating it and favoring differentiation. Marginal habitat on the western Highland Rim would have been instrumental in this scenario in preventing contact of these two forms at the confluence of the Duck and Tennessee rivers.

Since the origins of these species, there have been several minor modifications of their ranges. Adjustments in the range of *E. squamiceps* include the elimination of the northern part of its range by glaciation and its invasion of the Red River system (Cumberland Dr.) presumably via stream capture.

Distributional changes in *E. neopteron* include dispersal south through tributaries of the Tennessee River into northern Alabama (with some differentiation) and east into the lower Duck River after the connection of the Tennessee-Duck drainages in the Pleistocene. Many of these streams have marginal habitat and populations are low. Mississippi Embayment populations have been eliminated except for those in the Bayou de Chien of western Kentucky (Fig. 14).

Modifications of the range of *E. crossopteron* include invasion of the upper Caney Fork via stream capture from the Duck River (also known for several other taxa), invasion of Cypress Creek (middle Tennessee drainage) via stream capture from the Duck River, movement west onto the western Highland Rim, where habitats are marginal and populations are low, and elimination of most of the populations in the Mississippi Embayment. After the Ohio River was diverted south into the stream bed of the Cumberland and the Mississippi River was diverted east to join the new Ohio River near Cairo, Illinois, the changed size and nature of the river and its floodplain would have adversely affected populations of *E. crossopteron* living in the small creeks immediately adjacent to the original river. The only population remaining is in a few small creeks near Reelfoot Lake in northwestern Tennessee (Fig. 9).

Etheostoma nigripinne has spread east throughout most of the Elk River and tributaries of the Tennessee as far as the lower Paint Rock River in northwestern Alabama, and north into tributaries of the Tennessee River as far as the mouth of the Duck River. Populations present in the upper Duck River (Bedford and Coffee Counties) may represent introductions via stream capture within the eastern Highland Rim between the upper Elk and Duck rivers. In this region headwaters of these two drainages interdigitate considerably and the divide is minor. Alternatively, these populations may indicate previous dispersal throughout the Duck system. Whatever the case this phenomenon is not unique to *E. crossopteron* and *E. nigripinne* since sympatric occurrences of two forms of *Noturus elegans* (Etnier and Jenkins, 1980) and *E. duryi* and the "golden snubnose darter" (Etnier, pers. comm.) are known from the Duck system.

Etheostoma olivaceum is the only species which has been unable to expand its range significantly. It is blocked on the east by the Cumberland

Plateau escarpment and on the west by possible competition with *E. crossopteron*.

Etheostoma virgatum group.—The distribution patterns of this group are complex (Fig. 17) and as noted earlier the geological history of this region is poorly known. Thus, our interpretation of the biogeography of this group with reference to its evolutionary history (Fig. 19) is difficult. The origin of the ancestral barcheck species was presumably in the ancestral Cumberland drainage since most primitive members of the subgenus (*obeyense* and *virgatum*) both occur in this drainage and the two species occurring outside the Cumberland are closely related to *E. smithi* in the Cumberland drainage. The easiest geological event to correlate with the evolutionary history of this group is the formation of the Nashville Basin. This event was probably closely tied to the origin of the ancestral species of *E. smithi*, *E. striatulum* and *E. barbouri*. Prior to the formation of the Nashville Basin the ancestral species of this group plus *E. virgatum* was widespread in the middle Cumberland River on the Highland peneplain. Once the basin hollowed out *E. virgatum* became isolated from the basin form, presumably being left on some part of the existing Highland Rim. Later in the Pleistocene, stream capture within the basin introduced a population into the Duck system which later differentiated into *E. striatulum*. It is possible that this capture was also involved in introducing the Cumberland ancestor of *E. crossopteron* and *E. nigripinnus* into the Duck system.

The origin of *E. barbouri* in the Green River system could have been correlated with a possible stream capture across the middle Cumberland-Barren divide, introducing the ancestor of *E. barbouri* into the Green system. Alternatively, the origin of species of this species pair (*smithi* and *barbouri*) could have been correlated with glacial processes fracturing the range of a once more widespread ancestral species inhabiting the lower Cumberland, Green River system, and tributaries of the Ohio River in intervening areas. Glacial outwash and lakes in the area of the present lower Ohio and Green rivers could have eliminated populations of the ancestor of these species in the lower Green and Ohio tributaries, thus promoting their differentiation.

Events correlated with the early origins of *E. obeyense* and *E. virgatum* are difficult to determine. *Etheostoma obeyense* could have been an isolate on the Cumberland Plateau when the ancestor of the remaining barchecks (Fig. 19) moved down over the 100 meter escarpment onto the Highland Rim peneplain. Because populations of this species are also known from the eastern Highland Rim, this scenario necessitates its later dispersal downstream. Alternatively, *E. obeyense* may have evolved on the eastern Highland Rim and later dispersed up onto the Cumberland Plateau.

Page and Schemske (1978) suggested that the distribution of *E. virgatum* in three segments of the Cumberland River drainage may indicate that this species was once more widespread and these populations represent relicts. If *E. virgatum* is a single species and was once more widespread we cannot address events leading to its initial differentiation.

Alternatively, it is possible that *E. virgatum* evolved in one of the main tributaries of the Cumberland River (in the Nashville Basin, eastern Highland Rim or Cumberland Plateau) and dispersed to other drainages. Because *E. virgatum* occupies a wider range of habitat types than most other barcheeks, it seems possible that it could have originated on the eastern Highland Rim in possibly the Caney Fork system when the Nashville Basin was formed and has subsequently spread down into the basin and up onto the Cumberland Plateau.

In summary, the early ancestors of the barcheck group may have been distributed on the Cumberland Plateau. Movement down onto the Highland Rim peneplain in the late Tertiary isolated *E. obeyense* from the ancestor of the remaining species. *Etheostoma virgatum* may have differentiated from the ancestral species of the remaining three taxa when the Nashville Dome hollowed out to form the Nashville Basin, leaving the former species on the eastern rim and the latter ancestor in the basin. The origin of *E. virgatum* may then have been correlated with the origin of *E. olivaceum*. *Etheostoma striatulum* was next temporally and became isolated in the Duck system via stream capture between the Cumberland and Duck in the basin. This event may have been correlated with the entry of the *crossopterum-nigripinne* ancestor into the Duck. The origins of *E. smithi* and *E. barbouri* may have resulted when glaciation fractured the range of a more widespread species into lower Cumberland and upper Green River populations, respectively. Alternatively, *E. barbouri* may have evolved in the upper Green River after a population of the ancestor of these two species was captured from the ancestral Cumberland drainage.

Adjustments of the distributions of *E. smithi* since its origin include possible dispersal into tributaries of the lower Cumberland River (given that the latter of the above two scenarios for the origin of this species and *E. barbouri* is accepted) and the invasion of some tributaries of the lower Tennessee via stream capture or dispersal as hypothesized by Starnes and Etnier (in press) (Fig. 17). A likely location for stream capture between the Cumberland and Tennessee rivers would be White Oak Creek (Tennessee drainage) and Yellow Creek, a tributary of the Cumberland. *Etheostoma smithi*, a large river and reservoir tolerant species, could have dispersed into the lower Cumberland drainage.

Alterations of the range of *E. virgatum* might have included downstream invasion of the Stones, Harpeth, and Red rivers and upstream dispersal into the Rockcastle River. Given that the origin of *E. barbouri* included a stream capture, it has experienced considerable dispersal since its origin. Modifications of the range of *E. striatulum* have apparently only included reduction of its range. Page (1980) and Kuehne and Barbour (1983) noted that populations of this species have been reduced due to agricultural practices.

Etheostoma flabellare group.—Until work on the undescribed species of this group and an analysis of the variation of *E. flabellare* is completed it is impossible to discuss much about the zoogeography of this group. However, their ancestral species must have been widespread and consider-

able dispersal, largely on the part of the widely tolerant *E. flabellare*, has occurred. One possible explanation for the origin of these two species is that *E. flabellare* evolved in the Teays-Mississippi system and *E. kennicotti* in the preglacial Ohio-Cumberland drainage. The hypothesis of a widespread *E. flabellare* was also considered by Pflieger (1975). Neither species was present in the middle and upper Tennessee prior to the connection of this drainage with the Duck-Cumberland drainage in the Pleistocene since no relatives occur in the Mobile Bay drainage and would likely be represented there given that either form was present at the time of the Tennessee R.-Coosa R. connection. Once the Ohio River was diverted south into its present location during the Pleistocene, *E. flabellare* gained access to the Cumberland and Duck drainages. Later in the Pleistocene when the Tennessee united, access to the middle and upper portions were available for both species.

Comparative Biogeography.—Historical events involved in the evolution of *Catonotus* are not unique to this group. Several other darters, particularly the subgenus *Nanostoma* (*sensu* Page, 1981), appear to have experienced a similar history. Relationships of species in these groups, however, are not as well known as in *Catonotus*. Within *Nanostoma*, *E. barrenense* and *E. rafinesquei* (Page and Burr, 1982) together are congruent with the distribution of *E. barbouri* and are partially congruent with *E. squamiceps*. Other species endemic to the Green River system include the fishes *Moxostoma* (*Thoburnia*) *atripinne* and *E. bellum*, and the crayfish *Barbicambarus cornutus* and *Orconectes barrenense* (Page and Burr, 1982). Based on results from the present study we would predict that these species would have their closest relatives in the Cumberland, lower Ohio, and perhaps Tennessee rivers. Within the subgenus *Thoburnia*, however, there are only two other species, both found in Atlantic Slope drainages. Results from a phylogenetic study of this group (Buth, 1979) indicate that the two east coast species are most closely related, and *M. atri-pinne* forms the sister group to these. Thus, at least within this group some extinction may have occurred. Relationships of *E. bellum* are not as thoroughly resolved but Zorach (1968) considered this species close to *E. ruffilineatum* of the Cumberland and Tennessee rivers and later (Zorach, 1972) placed it in the species group with *E. camurum* of the Ohio, Cumberland, and Tennessee rivers and *E. chlorobranchium* of the upper Tennessee.

Other darter species have striking distributional similarities with species of *Catonotus*. *Etheostoma emieri* and *E. olivaceum* in the Caney Fork River; the "golden snubnose darter" and the pair *E. s. simoterum* and *E. s. atri-pinne* with the species pair *E. crossopterum*-*E. nigripinne*, except that *E. nigripinne* does not ascend the Tennessee River as far as *E. simoterum*; *E. duryi*, *E. jessiae*, and *E. nigripinne*, except again the latter does not extend as far upstream; the "red snubnose darter" and *E. neopterum*; and *E. microlepidum* of the Cumberland, *E. aquali* of the Duck and *E. sp.* of the Elk (Williams and Etnier, 1978) with *E. crossopterum* and *E. nigripinne*. Although relationships of these species

are not fully resolved and distributions of some are not exactly the same, primarily due to habitat differences, it will be interesting to see how much congruence with the subgenus *Catonotus* is observed.

HABITAT AND COMPETITION

In addition to geological and drainage histories of a region determining species ranges in *Catonotus*, habitat association and competition with congenieries may have had a profound effect on the distributions of these species. This aspect of *Catonotus* biogeography has also been discussed by Page and Schemske (1978). Each species group in *Catonotus* can be characterized as having a preferred habitat, although there is variation within groups and even within a species. This is somewhat at variance with ideas presented by Page and Schemske (1978); our interpretations are stated below. The *flabellare* group prefers sand or gravel pools and gravel riffles while the *squamiceps* and *virgatum* groups prefer slab or bedrock pools. Table 15 lists the habitat preferences of the different *Catonotus* species based on collections from over 400 localities (MEB). We suggest, therefore, that these designations represent the normal habitats for each species. In fall and winter, however, strays may be found in any habitat. Since breeding locations of some species and populations are unknown, it is also possible that they migrate to different habitats for spawning. For example, whether populations of *E. kennicotti* and *E. neopterum* in sandy creeks have modified their spawning behavior or whether they migrate to an area with flat rocks is not known.

Throughout most of the Green, middle and lower Cumberland, and middle and lower Tennessee rivers, members of each species-group are generally allopatric but often are sympatric with a representative of another *Catonotus* species group. Although *E. kennicotti* and *E. flabellare* commonly occur together, there are no records of any two members of the *virgatum* group occurring together, and instances of sympatry between members of the *squamiceps* group are rare.

Etheostoma flabellare group.—*Etheostoma flabellare* is the only true riffle inhabiting *Catonotus* and is the most widespread in distribution. Although sympatric with all other *Catonotus* (Table 16) it is not truly syntopic with any and therefore would presumably not be in direct competition.

Page and Schemske (1978) hypothesized that the absence of *E. kennicotti* in the lower Cumberland River drainage is a result of its failure to compete successfully with other pool inhabiting *Catonotus*. We believe this to be only part of the explanation. Since *E. kennicotti* is known to occur with *E. flabellare*, *E. barbouri*, *E. squamiceps*, *E. nigripinne*, and *E. neopterum*, competition with other *Catonotus* must not be the most important factor in determining its distribution. In fact, *E. kennicotti* rarely occurs without at least one other *Catonotus* being present. The total number of *Catonotus* species inhabiting the region does not seem to limit the occurrence of *E. kennicotti*. Although seven species of *Catonotus* inhabit the middle and lower Cumberland River no more than three are

TABLE 16. Sympatric populations of *Catonotus* species. X=sympatric population, ?=probable sympatric distribution based on literature reference or ranges.

Species	<i>flabellare</i>	<i>kennicotti</i>	<i>squamiceps</i>	<i>neopterum</i>	<i>olivaceum</i>	<i>crossopterum</i>	<i>nigripinne</i>	<i>obeyense</i>	<i>virgatum</i>	<i>striatulum</i>	<i>smithi</i>	<i>barbouri</i>	TOTALS
<i>flabellare</i>		X	X	X	X	X	X	X	X	X	X	X	11
<i>kennicotti</i>	X		X	X		?	X	?				X	5(7)
<i>squamiceps</i>	X	X										X	3
<i>neopterum</i>	X	X				X	X						4
<i>olivaceum</i>	X												1
<i>crossopterum</i>	X	?		X					X	X	X		5(6)
<i>nigripinne</i>	X	X		X									3
<i>obeyense</i>	X	?											1(2)
<i>virgatum</i>	X					X							2
<i>striatulum</i>	X					X							2
<i>smithi</i>	X					X							2
<i>barbouri</i>	X	X	X										3

found in any one stream and *E. kennicotti* occurs with at least that many species in the Green River System (*squamiceps*, *flabellare*, *barbouri*). If competition with other *Catonotus* is not sufficient to explain the distribution of *E. kennicotti* perhaps the answer is competitive interactions between *E. kennicotti* and other darters. Throughout most of its range, *E. kennicotti* prefers sand and gravel pools (Table 15), but in the upper Cumberland, upper Tennessee and Shawnee Hills it also inhabits slabrock pools and sometimes gravel or rock riffles. In these areas, there are few species of darters and competition could be minimal. For example, in the Tradewater River (Shawnee Hills), the only common darters are *E. kennicotti*, *E. squamiceps*, and *E. nigrum*; thus *E. kennicotti* and *E. squamiceps* are ubiquitous in these streams, inhabiting most pools and riffles. *Etheostoma kennicotti* inhabits the upper Green River, but is absent from the Barren River—a system rich in darter species. Likewise *E. kennicotti* occurs in some areas of the Buffalo, but not the rest of the Duck River System. Probably *E. kennicotti* (or the ancestral species) was primitively a slab rock species, but switched to a sandy or gravel pool habitat (at least for most of the year), except at localities lacking competitors where it reverts to its ancestral habitat.

Etheostoma squamiceps group.—Distributions of members of the *squamiceps* group are apparently not affected by competition with members of other species groups. *Etheostoma squamiceps* species occur sympatrically with all other *Catonotus* except *E. obeyense* and occur syntopically with all of these species except *E. flabellare*. Within their own group, however, competition may be the most important factor limiting species distributions. Except for *E. neopterum*, members of this group have the same preferred habitat, shallow pools, usually with a bedrock substrate, containing flat slab rocks. *Etheostoma crossopterum* and *E. nigripinne*

have less rigid requirements than *E. squamiceps* and *E. olivaceum* and are sometimes found in small numbers in gravel or sandy pools. Apparently, however, no two slab rock species can exist syntopically, as is similarly observed in the slab pool inhabiting species of the *virgatum* group. Although *E. crossopterum*, *E. squamiceps*, and *E. olivaceum* inhabit the middle and lower Cumberland River drainage and *E. crossopterum* and *E. nigripinne* inhabit the Duck River, no mixed collections are known. *Etheostoma neopterum* is the only exception to this generalization. The preferred habitat of *E. neopterum* is sandy streams, a habitat where no syntopic occurrences with other members of the *squamiceps* group species are known. Mixed collections of *E. neopterum* and *E. crossopterum* or *E. neopterum* and *E. nigripinne* occur in gravel bottom streams—a habitat marginal for both species. Apparently, neither species can attain high enough population levels in these marginal areas to exclude the other species. It is noteworthy that *E. neopterum* has the most distinctive breeding characteristics of any species of the *squamiceps* group and thus could probably co-exist with less chance of any interspecific mating.

Etheostoma virgatum group.—The distributional pattern of barcheek darters is unusually compact but complex (Fig. 17). Three of the five species are nearly sympatric in the middle and lower Cumberland River drainage. The remaining two species, *E. barbouri* and *E. striatulum*, occur only in the Green and Duck river systems, respectively. *Etheostoma obeyense* and *E. smithi* occupy the same microhabitat—small, permanent, quiet, bedrock bottom creeks where they hide under flat rocks, among emergent vegetation or in cracks in the bedrock. *Etheostoma obeyense* inhabits streams on the eastern Highland Rim and *E. smithi* in the Nashville Basin and the western Highland Rim. *Etheostoma virgatum*, if a single species, is more versatile, occupying habitats ranging from small intermittent creeks to fairly large rivers. It may also inhabit slab rock pools, gravel bottomed pools or quiet gravel riffles. Apparently *E. smithi* may exclude *E. virgatum* from some areas, but specialized habitat requirements limit its distribution to small direct tributaries of the Cumberland River. The most important limiting factor seems to be riffles. Larger streams and those creeks on the eastern slope of the Nashville Dome have long gravel riffles, some of which are quite rapid. Because of its large size and wide habitat tolerance, *E. virgatum* can bypass these riffles and invade areas not occupied by *E. smithi*. Thus, *E. virgatum* occupies large tributaries (Red, Harpeth, Stones, Caney Fork rivers) while *E. smithi* is found in the smaller, quiet tributaries. Page and Schemske (1978) describe the ranges of *E. smithi* and *E. virgatum* as relictual—remnants of formerly wide ranges. It is also possible that their distributions represent dynamic equilibrium between two competing relatives and is the result of recent expansion of ranges rather than contractions. One interesting situation is the distribution of *E. smithi* and *E. virgatum* in the Stones River. *Etheostoma virgatum* is common throughout the lower river and West Fork while *E. smithi* is found in only two tributaries of the East Fork. This represents the only population of *E. smithi* in a large tributary

of the Cumberland River. In 1967, extensive collecting in Bradleys Creek, one of the known *E. smithi* localities, failed to reveal any barcheeks. In 1978 additional collections in this region indicated that *E. smithi* was common at the same localities. Between 1967 and 1978, the Percy Priest Reservoir was constructed on the lower Stones River and the lake extends almost to the *E. smithi* localities. Perhaps habitats created by the lake gave *E. smithi* a chance to bypass the expansive riffles which formerly acted as barriers. It will be interesting to see if this species spreads throughout the rest of the Stones River system.

The distribution of *E. obeyense* is much harder to interpret. Apparently, it can exclude *E. virgatum* just as *E. smithi* can, and because of its larger size, can inhabit larger streams. Thus, *E. obeyense* may have kept *E. virgatum* from the South Fork and Obey rivers, they only sizeable tributaries of the middle and lower Cumberland drainage where *E. virgatum* is lacking. The Cumberland Plateau escarpment acts as a barrier on the east for *E. obeyense* but the barrier against westward expansion is unclear. Competition with *E. smithi* is a possible explanation although there is a hiatus of several kilometers between their two ranges.

Factors regulating the distribution of *E. barbouri* and *E. striatulum* apparently are historical rather than biological. Both species are the only *virgatum* group members in their respective areas, although both occur syntopically with other pool inhabiting *Catonotus* and competition with other barcheeks is not a factor in explaining their present distributions. *Etheostoma barbouri* occurs throughout the Green and Barren rivers wherever suitable habitat is present. *Etheostoma striatulum* inhabits every permanent tributary of the Duck River in the Nashville Basin, but has been unable to move out of the Basin onto the Highland Rim even though some streams appear to have suitable habitat.

In reviewing ecological preferences, distributions, and competition between species of *Catonotus*, the following pattern emerges:

1. The ancestral *Catonotus* species inhabited slab rock pools.
2. Interspecific competition importantly affects distributions within species groups, but members of different species groups often occur syntopically.
3. Within species groups, sympatry is most likely between species with a long evolutionary separation, and with some habitat and secondary sexual divergence.
4. The species having the largest ranges (*flabellare*, *kennicotti*, *virgatum*) owe their "success" to modified habitat preferences that minimize competition with other *Catonotus*. *Etheostoma flabellare* has shifted from a pool to a riffle habitat and has been most successful in expanding its range. *Etheostoma kennicotti* and *E. virgatum* are less dependent on a specific habitat and flexible enough to use any areas not already occupied by other *Catonotus*. This flexibility was accompanied by a loss of competitive advantage within any one habitat and both

species are strongly influenced by competition by other *Catonotus* species as well as other species.

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APPENDIX 1

Characters and implied transformations used in the phylogenetic analysis of species of *Catonotus*. The condition listed first and generally coded as 0 is considered primitive in *Catonotus*. See text for explanations of implied transformations.

1. Genital papillae of females: tubular, conical = 0, flat and not bifurcate = 1.
2. Spawning location: in gravel = 0, on undersides of slab rocks = 1.
3. Dorsal fin shape: high and rounded edge = 0, low and straight edge = 1.
4. Knobs on first dorsal fin: absent = 0, large = 1, small = 2.
5. Head of breeding males: not swollen = 0, swollen = 1.
6. Infraorbital pore 4: present = 0, absent = 1.
7. Lateral line: completely pored = 0, < 75% pored = 1, < 45% pored = 2, < 40% pored = 3, < 35% pored = 4, < 30% pored = 5, < 20% pored = 6.
8. Habitat preference: gravel riffle, raceway = 0, slabrock pool = 1, sand-gravel pool = 2.
9. Nape squamation: scaled = 0, naked = 1.
10. Prepectoral squamation: scaled = 0, naked = 1.
11. Opercle squamation: scaled = 0, naked = 1.
12. Cheek squamation: scaled = 0, naked = 1.
13. Suborbital bar: strongly developed = 1, absent = 0, weakly developed = 2.
14. First dorsal fin pigmentation: orange band present = 1, no orange band, but similar in other respects = 2, reds and black basoanterior spot = 0.
15. Infraorbital pore 3: present = 0, absent = 1.
16. Iridescent red and white cheek bar: absent = 0, present = 1.
17. Preopercle edge: entire = 0, crenulate = 1.
18. Longitudinal stripes on flanks: absent = 0, present = 1, strongly developed = 2.
19. Infraorbital pore 2: present = 0, absent = 1.
20. Infraorbital pore 5: present = 0, absent = 1.
21. Caudal spots: absent = 0, present = 1.
22. Rays of second dorsal fin: extending only to fin margin = 0, extending well beyond fin margin = 1.
23. Windows in first dorsal fin membranes: absent = 0, present = 1.
24. Number of eggs spawned by a female at a time: one = 0, greater than one (usually 3) = 1.
25. Female spawning behavior: inverted for extended period of time = 0, inverted briefly = 1.
26. Tips of rays of second dorsal fin: pointed = 0, expanded into large knobs = 1.
27. Branches of rays of second dorsal: separate = 0, adnate (appearing unbranched) = 1.
28. Tips of second dorsal fin rays: white = 0, black = 1.
29. Modal number of pectoral fin rays: 12 = 0, 11 = 1.
30. Knobs on first dorsal fin: normal = 0, greatly enlarged = 1.
31. Color of knobs on first dorsal fin: opaque or white = 0, golden = 1.
32. Sexual distribution of first dorsal fin knobs: typically males only = 0, males and females = 1.
33. Modal number of dorsal fin spines: 9 = 0, 8 = 1, 7 = 2.
34. White lines in second dorsal fin: concave = 0, tending to form horizontal dashes = 1.
35. Modal number of anal fin rays: 8 = 1, 7 = 0, 9 = 2.
36. Modal number of dorsal fin rays: 13 = 0, 12 = 1.
37. Modal number of dorsal fin rays: 13 = 0, 11 = 1.
38. Modal number of dorsal fin rays: 13 = 0, 14 = 1.
39. Second dorsal fin color pattern: submarginal colored = 0, submarginal region with broad, white band = 1, submarginal region black = 2.
40. Preoperculomandibular pores: 10 = 0, 9 = 1.
41. Clear basal band in first dorsal fin: present = 0, absent = 1.
42. Knobs on first dorsal fin: elongate = 0, round = 1.
43. Windows in membranes of first dorsal fin: round = 1, vertical slits = 0, ovals = 2.
44. Scales above lateral line: 4 = 1, 5 = 2, 6 = 3, 7 = 4.
45. Scales below lateral line: 7 = 1, 8 = 2, 9 = 3.
46. Modified fleshy ridges on ventrolateral scales of breeding males: absent = 0, present = 1.

APPENDIX 2

Characters used in phylogenetic analysis of the subgenus *Catonotus*. All characters are defined in Appendix 2 and discussed in Relationships. Character numbers and implied transformations correspond to numbers in Figure 19.

		CHARACTERS																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							
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